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THE BIOLOGICAL BASIS OF SOCIAL PROBLEMS[1]

INTRODUCTION

DR. S. J. HOLMES
UNIVERSITY OF CALIFORNIA

THE following papers were presented at a symposium held in honor of Professor William E. Ritter at the meeting of the Western Society of Naturalists, held at Monterey, Calif., December 20, 1939. In addition to the papers here published there was an interesting contribution by Dr. H. S. Jennings dealing with the social behavior of Paramecium, but it is not included here because arrangements had previously been made for its publication elsewhere. During the same meeting of the society another symposium was held in honor of Professor D. H. Campbell, who for many years has been professor of botany at Stanford University. The idea of holding symposia in honor of these two distinguished investigators who have long been prominently identified with the development of their respective branches of science on the Pacific Coast was a most happy one, and the dedication of a symposium on the biological aspects of social problems to Dr. Ritter was peculiarly appropriate because of his broad human interest in the social import of the biological sciences.

[1] Symposium on "The Biological Basis of Social Problems," held in honor of Professor William E. Ritter at the meeting of the Western Society of Naturalists, Monterey, Calif., December 20, 1939.

A FEW WORDS ABOUT NATURE[1]

DR. WM. E. RITTER
UNIVERSITY OF CALIFORNIA

IT has seemed to me that this meeting of a group of professed naturalists should be a fit time for some brief, easy reflections on what is meant by the terms *nature, natural, naturalist,* etc. I have lately become impressed by the great variety of usage of these words. What is the meaning of the familiar phrase that such and such an object or act is "perfectly natural," or the almost equally familiar phrase, "Let nature take its course"—common even in economics and business? And what does a philosopher or theologian mean by the "nature of God" or of the "soul" or of the "spirit"?

How many of us here are aware that a few dyed-in-the-wool philosophers, especially in our country, are declaring themselves to be naturalists, even though no one of them seems quite to agree with any of the others? So time-honored, if for no other reason, is *naturalist* as used by groups like this that it would appear only *natural* for us to feel ourselves somewhat competent if not obligated to contribute a bit to the clarification of this bewildering situation.

For myself, I eagerly acknowledge my indebtedness to W. K. Brooks for a suggestion that has grown in significance with me. Brooks is reported on unquestionable authority to have remarked once in a conversation that there seems to be a misunderstanding about the term "supernatural," for, he said, "Nature is everything that is." After much reflection I have ventured to modify this somewhat, though keeping, I am quite sure, to the spirit of Brooks's statement. My modification has been merely to bring the idea into fuller accord with the idea of time. The "is" of Brooks's expression is obviously, it would seem, more restrictive to the "now"—to the "present"—than he, a zoological evolutionist, would stand for. Here is my revision: Nature is everything

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that is, everything that has been and everything that will be—so far, that is to say, as we have any trustworthy information and understanding.

The main implications of this as to the Natural Sciences is clear. Geography, geology, meteorology and astronomy, also physics and chemistry range themselves at once as natural sciences no less than do botany and zoology; anatomy, physiology and ecology; embryology, genetics and biology. That is all obvious and easy. But what about the vast display of the Humanities—well so named? What about man's language and art; government and other social phenomena; knowledge itself including science; philosophy, ethics and religion? Are all these included in Nature? Here is where the shoe pinches. And the pinch is too tight and difficult for such a nursling naturalist as I am to adjust, especially in a "few words."

Here, then, are the last of my few words:

(1) Reinstate in the idea of biology the meaning it would have if true to the word *bios* with the meaning it had to its originators, the Greeks. This done, the title of the symposium with which you have graciously honored me would be essentially as follows: "That Portion of Biology Which Deals with Social Problems." The slight attention that is given by us moderns to the historic and lexicographic fact that *bios* as used by the Greeks meant "the way of life, especially of men" is strange. For example, "Bios Ellados" was the title of a treatise on Greek civilization written by a historiographer of the later Aristotelian school. This is our illustration from the ancients. Now for a thoroughly modern illustration: E. W. Scripps, certainly one of the brainiest men I have ever known, evolved the idea from his own general experiences, with no coaching from the outside, that he wanted to form a department of sociology in the biological institution at La Jolla, now the Scripps Institution of Oceanography. In accordance with these views hardly anything is more unfortunate for modern culture and civilization than the very prevalent conception that human society is not natural in the same sense that hymenopterous or avian societies are natural. For

seemingly, this conception is largely responsible for the doctrine that social science is not, nor ever can be, natural science.

(2) View nature in this revised Brooksian fashion; notice also how it is adumbrated by the labors of a few such persons as Aristotle, Confucius-Mencius, Marcus Aurelius, Spinoza, Goethe and above all by Charles Darwin, and you will not (if your experience is like mine) see the slightest ground for conceiving something utterly different from, or outside of, nature as the reality by which we are certainly surrounded every moment of our lives, and upon which our coming into existence and continuance therein are certainly dependent. You will feel no need or desire for some goodness thus exterior to nature, nor any dread or fear of some evil similarly exterior. In a word, this conception of nature leaves, for me at least, no place whatever for such an idea as the supernatural, even though this be garbed in such beguiling terms as metaphysical and metaphysics.

In view of the fact that ethics and religion received special attention as social factors in the symposium, I probably ought to be more specific about these in such a view of nature as I have sketched.

When human nature has been analytically studied as thoroughly as the rest of nature has been and is being studied by the natural sciences, and also synthetically studied as thoroughly as traditional philosophy had erroneously supposed it was studying them, it will be found that the basic factors of both the emotional and rational nature of the human species which make the species moral and religious, should by further development do more for the good of the species than is possible on the basis of any theory or belief in supernatural factors of any kind or name.

To be rid of supernaturalism in every aspect of human life, not by explicitly rejecting it, but by such a development of naturalism that there shall be no longer any need or room for supernaturalism, is the great stage of cultural evolution in which the human species is now struggling.

SOCIAL INTEGRATION AS A BIOLOGICAL PROCESS[1]

PROFESSOR C. M. CHILD
STANFORD UNIVERSITY

IT has been debated, sometimes with considerable vigor, whether the social group or unit is to be regarded as an organism. A parallelism has been drawn between the organs of the biological organism and the differentiations within a society or social group and between the division of labor in the organism and society. On the other hand, it has been pointed out that there is physical continuity in the organism, but not in society. It has been maintained, mistakenly it appears, that society has nothing corresponding to the sensory apparatus and the central nervous system of the organism. The psychological factor in human society has often been regarded as rendering any comparison between a society and an organism without significance. Whether we call a social unit an organism or not does not appear to matter greatly. It is, however, a fact of some significance that neither the biologist nor the sociologist is able to avoid use of the term "organization" both as a process and as a condition, and the term apparently has much the same significance for both. As commonly used, it means development or presence of a definite orderly pattern with definite relations of its parts. In the organism the development of this pattern involves a physiological integration of some degree and kind, which makes the organism in some measure a unity. Integration involves development or presence of more or less difference in the parts integrated in both organism and society. Integration and differentiation are both features of organization; integration, either in organism or in society, is impossible without difference of some degree or kind in the parts or individuals to be integrated. The present purpose is merely to call attention to some of the rather striking

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similarities between physiological integration and social integration.

In the organism two groups of factors are concerned in integration: First, occurrence of energy transformations and transmission of their effects without mass transport of substance from the point of origin to that of effect. The chief of these factors is excitation of living protoplasms and its transmission, either through or along the limiting surfaces of protoplasms, or with more advanced differentiation, by means of nerves. Protoplasmic transmission in the absence of special transmitting organs, the nerves, is usually not very effective, as compared with nervous transmission, and its range of effectiveness is commonly more or less limited. Nervous transmission is more effective, and in the nerves of higher vertebrates its range of effectiveness appears to be limited only by the length of the nerve. The second group of factors concerned in physiological integration is production, transport and effect of particular substances; the various hormones are conspicuous in this group.

Local excitation by some external energy and its transmission can occur without preëxisting difference of the parts concerned. The primary excitation establishes a difference, at least for the time being, and in consequence dominates or controls the parts to which it is transmitted. For a production of a particular substance by a particular part and a particular effect of it on some other part or parts, the two parts must already be different in some way and to some degree. If both are producing the same substance at the same rate it does not become an integrating factor. If one is producing it at a higher rate than the other, that is, if the difference between the two parts is quantitative, there may be some integrating effect of its transport from the former to the latter. The increase in concentration in or about the latter may inhibit production there because of the difference in physiological condition, or perhaps alter the course of reactions otherwise. In any case, it is evident that these material factors, hormones, etc., do not represent the most primi-

tive sort of physiological integration. For that we must look to excitation and its transmission for which no preëxisting difference in the parts concerned is necessary. For localized production and effect of material factors an organization pattern of some sort must already be present. It does not necessarily follow, however, that physiological integration always begins with excitation and transmission.

Essentially the same two groups of factors are concerned in social integration: First, communication, which is really transmission of excitation by one means or another, by voice and hearing, by reaction through vision to behavior of others, to books, to factors in external environment, and so on. The media of social communication are not protoplasmic; they may be air, the telegraph, the telephone, the written or printed word, but they represent transmission, not transport. Moreover, many of them, like the nerves of organisms, are fabrications of living protoplasms.

The other group of factors in social integration is material production and exchange, the commercial factors. As in the organism, these material factors play no part socially until some degree or kind of differentiation or pattern is present. If all persons in a group produce or obtain the same amounts of the same substances there can be no commercial relation between them. If some have more, others less, an integration may result in which the latter receive from the former, but if some are agriculturists, others hunters or fishermen, barter and exchange, regular commercial relations become possible, but these relations depend on communication.

Analysis of these integrative relations in organisms and society shows that they are relations of some degree of dominance and subordination, of control and of being controlled. Both transmitted excitation and transported substances exercise control in organisms. Both communication and commercial relations are controlling factors in social integration. Experiment shows that in many of the simpler axiate animals integration is more or less

completely autocratic in character, so far as development and structure are concerned, that is, control in development is largely or wholly a one-way relation and this control is associated with the physiological activities which we call metabolism. Along the polar axes of such organisms we find evidences of a gradation in rate of metabolism, and the region in which rate is highest is dominant and to a high degree independent of other parts. So far as behavior and structure are concerned, removal of other parts has little or no effect on a hydroid hydranth or a planarian head. The hydranth may finally die from lack of oxygen because other parts are not present to support it free above the substrate and the head may die of starvation, but each remains what it was. Very similar situations as regards autocratic or oligarchic governments cut off from their subordinate populace are not far to seek in human history. In these forms, however, isolation of other parts from the hydranth or head affects both their behavior and structure; as will appear, they are badly handicapped until a new dominance arises and again establishes order.

This autocratic type of dominance in hydroids, planarians and various other forms is usually limited in range of effectiveness, that is, communication is not good. Probably under the conditions it is the only type of dominance that can maintain a fair degree of integration in these forms. However, it is usually not completely successful and physiological isolation, that is, escape from control, occurs frequently in parts most distant from the dominant region. This escape may result from increase in length of the body, from decrease in effectiveness of dominance by weakening, aging or inhibition of the dominant region, by blocking of passage of the effective factor, or by activation of a subordinate part by some external factor to such a degree that it becomes insensitive to the control of the dominant region.

All of these situations are paralleled in human relations. The group may become too large to be controlled, particularly if communication is poor, the autocrat may

become old or ill, his decrees may fail to reach the more distant parts of his domain because of flood, earthquake or failure of the messengers, or local conditions may arise in a less completely subordinated part of the group, resulting in rebellion and a declaration of independence.

A new dominance usually develops from the most active region of the physiologically isolated part, that is, the portion of it which reacts most rapidly or most intensely to the altered situation establishes a new government. Human society affords plenty of parallels for this situation. Except in primitive societies, rebellion, or active separation, is perhaps the most common factor in the social field. In the organism the new dominance is essentially of the same type as the old; there is no improvement in the government. Socially there may or may not be improvement.

As regards initiation and establishment of dominance most eggs give us little information. At the beginning of embryonic development the egg usually has a definite pattern of organization, presumably established during its ovarian history, and in the so-called mosaic eggs this organization approaches that of a well-established social group in which every member knows what he has to do for some time to come. Buds and reconstitution of isolated pieces of the simpler animals bring us nearer to the beginnings of developmental pattern. Here only certain of the reconstitutions need concern us. Reconstitution of isolated pieces of hydroids, planarians, many annelids and various other forms presents certain interesting aspects of dominance which again are not very different from happenings in social groups. In general, whatever the body level from which a piece is isolated, that part of it nearest the original dominant region undergoes activation following the isolation, becomes a new dominant region and induces reorganization in other parts of the piece. This new dominant region becomes the hydranth or the head, but it is more or less dominant before it differentiates, though its dominance may not be fully effective until it reorganizes the means of communication, that

is, the nervous system. In other words, with physical isolation from the original government a new government arises and brings about more or less extensive reorganization in other parts. Here, as in physiological isolation, it is a government of the same kind as the original, and an individual of the same kind results. In the hydroid and the planarian the dominant region is self-differentiating; it can develop in complete absence of other parts. If it fails to develop because of inhibiting conditions, reorganization into a new individual does not take place; without the dominant region the piece can not give rise to anything above the body level from which it was taken; it possesses no initiative and remains only a piece.

Under certain conditions activation at both ends of a piece is sufficient to determine a dominant region at each end. Each of these induces reorganization until it is blocked by the reorganization induced by the other. Here two independent governments have arisen, each exercising control over a part of the piece. It is not difficult to find situations closely paralleling these reconstitutions in social integrations, isolations and reintegrations.

If a dominant region is grafted into some other part of the body it may develop quite independently of its position and bring about reorganization in the body of the host, even sometimes in both directions, distally and proximally or anteriorly and posteriorly from itself for a greater or less distance and in planarians, even when it is the dominant region of another species. In these cases of grafts the reorganization may involve complete obliteration of the original host pattern and reversal in direction of the order distal or anterior to the graft. This approaches a revolution in the parts concerned, but again the new government is of the same kind as the old.

In the course of progressive biological evolution there is approach to a more or less democratic type of organization, but with many halts and digressions on the way. In the mature higher vertebrate and human organism, for example, there is something like representative government. It has often been pointed out that the brain, more

particularly the cerebral cortex, functions as a sort of deliberative body acting on the messages it receives from other parts. The transportative or commercial relations among the parts, hormones, oxygen supply, nutrition, etc., play a role in determining the character of the messages and of the resulting action. Every part of such an organism can, on occasion, get a message through to the central deliberative body and if it is sufficiently important, action results. If something unusual happens to the part, it may become a pressure group, like some social groups with which we are familiar.

The simpler organisms with autocratic dominance show a characteristic particularly interesting in this connection. Any level of the body is capable of becoming a dominant region, provided it can escape from the dominance of another part. The autocratic government has not obliterated the capacity to dominate, if the opportunity is given. The functionally more or less democratic higher vertebrate, however, is, in mature stages, an integration with highly stable structure, like a long established democratic organization in which the class limits have become more or less fixed. The central deliberative body, the cortex, is functionally the most highly labile or plastic part of these organisms: If it ever loses this lability the evolution of human intelligence and, so far as human beings are concerned, social evolution, will probably be at an end. There is considerable evidence that dominance in the earlier embryonic stages of vertebrates, including man, is more or less autocratic in character and that the general structural pattern is largely determined by this type of dominance.

It is perhaps of some interest to note that the more completely communistic organism complexes, consisting of many similar zooids, have remained relatively primitive in character, the chief relation between components being nutritive. There may be dominance and subordination in each zooid member, but there is little or no integration or dominance of the whole.

It may perhaps appear that we have been largely con-

cerned thus far with physiological integration as a social process rather than with the reverse. So far as this is true, it is because this has seemed the simplest and most direct way of emphasizing the similarities of process as distinguished from mechanism. The mechanisms of physiological and social integration are, of course, quite different.

In processes of social integration all types and degrees of dominance appear. Dominance may reside in the personal leader—in the primitive group, the wise man, the old man, or the one who, by virtue or by vice of some characteristic, imposes himself as leader. The most persuasive talker, the greatest bully, the most lawless gangster, may dominate. A particular coincidence of conditions and personal character may determine leadership in an individual who, under other conditions, would have remained an inconspicuous member of the group. Such personal dominance may range from the purely autocratic to a democratic type in which the leader is accessible to all members of the group, may be advised by any or all, and acts or recommends on the basis of that advice; that is, integration in relation to a person may range from the type found in the hydroid and planarian to that of the higher vertebrate.

There is, of course, a psychological basis for social integration. Integration may result from fear of or respect for a person, or personal dominance may have a political or religious basis. But abstractions, concepts, symbols, even verbalisms, are dominant in many social integrations. An institution—the state, the church, the college, the school, the lodge, the club, the general purpose of a particular group—is often dominant as an abstraction, not infrequently as a word, and such dominance may be almost as autocratic as physiological dominance in hydroid and planarian development. In this case, however, the dominant factor in the integration exists only as an abstraction from the group itself, but it is none the less effective. Even the personal leader may become an institution, an abstraction, in the minds of members of the group which he dominates, and as such he may be more

completely dominant than as a person. On the other hand, the dominance of an institution may be democratic, permitting discussion, revision or shift of dominance, and between these extremes all gradations appear. As in the organism, with development of means of communication and transport, the effective range of social dominance increases greatly: The great nation-states with populations of millions spread over thousands of miles of territory are examples.

Is the parallelism between physiological and social integration a mere analogy between fundamentally different activities of living protoplasms? It seems to be more than that. Dominance does not originate autonomously, either in organisms or in social integration, not even when we implant a dominant region into some other part, nor when a personal leader imposes himself on a group. It originates as a reaction to something, as a feature of the behavior of living protoplasms. The basis of both physiological and social integration is the more general and fundamental, perhaps one may say, the more primitive reaction patterns of living protoplasms to physiological, social, or other factors in their environments. These reactions are determined by the potentialities and limitations of protoplasmic behavior. Human reactions are much more complex and varied than those involved in development and maintenance of hydroid or planarian pattern, or even of a human embryo, but they are after all realizations of the same general potentialities of reaction and subject to similar limitations.

If evolution is a fact, rather than an idle dream, similarity of the more general behavior expressions of living protoplasms, whether cells or human beings is no mere analogy, but an essential feature of evolution. Also, if evolution is a fact, the change in character of physiological dominance and integration from the autocratic toward the democratic type may perhaps make us a little more hopeful regarding the future of mankind in the course of biological time, even though the character of dominance in some of the social integrations of the present day is far from encouraging.

THE NATURALIST AS A SOCIAL PHENOMENON[1,2]

DR. FRANCIS B. SUMNER
SCRIPPS INSTITUTION OF OCEANOGRAPHY

I PRESUME that I have been included among the speakers in to-day's symposium merely for the reason that I am an old friend and admirer of Dr. Ritter's and not because I am really expected to contribute any ideas of importance on the "biological basis of social problems." Indeed, the title which I first suggested for this discourse was quite a different one from that which appears on our program. It was: "Is There Any Present-Day Need for a Society of Naturalists?" But Dr. Taylor readily convinced me that such a title would not harmonize very well with the general title of this symposium.

Nevertheless, the rhetorical question which I have just set before you springs from an obsession of mine of long standing, and this is such an insistent one that I shall devote a considerable part of my time to the attempt to answer it.

Let us consider first, however, some of the implications of the title actually adopted: "The Naturalist as a Social Phenomenon." The thought at once arises: How could the naturalist, or any other scientist, exist except as a social phenomenon? Leaving out of account the considerable cultural background which must develop before science is possible, it seems evident that the motivation of the individual scientist is necessarily largely social.

We as a group are often credited by idealistic writers, outside of our own profession, with a "disinterested love" of some abstraction called "Truth," or "Science," or what not. Of course we have too much sense to believe that sort of stuff ourselves. But we are, I think, prone to believe that we are actuated primarily, if not exclu-

[1] Read at a symposium on "The Biological Basis of Social Problems" held in honor of Professor William E. Ritter at the meeting of the Western Society of Naturalists, Monterey, Calif., December 20, 1939.

[2] Contribution from the Scripps Institution of Oceanography, New Series, No. 97.

sively, by our intellectual interest in what we are doing. How far is that really true?

I have confronted myself, and various of my colleagues, with some more or less embarrassing questions, which are not, I presume, altogether original with me. Would you keep on making these interesting observations if publication or any other outlet for your discoveries were denied you? I think that I hear an almost unanimous negative reply to the question. Frankly, it is the reply which I myself should give. I admit that the conditions suggested would be rather rough on you. So we'll let you publish your discoveries in full, but with the proviso that they shall always remain anonymous. No one but yourself would ever know the secret of their authorship. I have a strong conviction that you would still hesitate, and that if you really decided to go ahead, it would be with vastly diminished zest. At least, I may so speak for myself. Nor is this necessarily a confession of vanity or selfishness. It is merely another bit of evidence that even *Homo scientificus* is a gregarious species. Our satisfactions are derived largely from the approbation and sympathetic understanding of our colleagues, from the interchange of ideas and—in very varying degree, it is true—from the belief that this hard-won increase in knowledge is, on the whole, a good thing for mankind. This last assumption is, of course, the only justification for the public support of scientific work, and I believe that the assumption is fully warranted. But the degree to which the individual scientist is motivated by such considerations is certainly highly variable. It is only too evident that in extensive areas of the world at present, important fields of science are being exploited for purposes quite other than human welfare. However, we naturalists may take satisfaction in the knowledge that none of the discoveries which we make in our field lends itself very well to the butchery of our colleagues who speak some other language.

What, then, is the peculiar field of the naturalist? My

past remarks, for the most part, would apply equally well to scientists of any sort. I shall not bore you with any attempt to define this term. Several quite different meanings are attached to the word, as will be found by glancing into a dictionary. What I mean here by a naturalist will develop in the course of the ensuing remarks.

I fear that the word is one which too often arouses feelings of antipathy or contempt in the mind of the modern biologist. It is difficult to escape the popular caricature: a wizened, bespectacled individual, who spends his time sorting and naming pickled specimens or endless rows of insects—an eccentric whose chief outdoor diversion consists in sweeping the air with a butterfly-net or gathering snakes and spiders in his wife's cooking utensils. At best, we are apt to think of a naturalist as an unfortunate who has not been able to keep up with the procession of those who are making the real advances in biology. Indeed, we are wont to prefix the words "old fashioned" when we apply this term to anyone.

What, then, is a naturalist? To say that he is a person who concerns himself with natural history would not, I am afraid, be very helpful in clearing our friend's reputation. For the expression "natural history" even more suggests something altogether primitive and out-of-date —a pursuit suited only to children and amateurs. Indeed, we learn from "Webster's Dictionary" that this term is "now commonly restricted to a study of these subjects [zoology and botany] in a more or less superficial way, at least without making use of modern anatomical and analytical methods." And a glance at the endless popular volumes carrying the title of "natural history" would seem to bear out this statement.

Are we, however, forced to accept such a depreciation of a term which has had such long and honorable associations? Listen to the words of one of our greatest naturalists, William Morton Wheeler:

> History shows us that throughout the centuries, from Aristotle and Pliny to the present day, natural history constitutes the perennial root-stock or

stolon of biological science and that it retains this character because it satisfies some of our most fundamental and vital interests in organisms as living individuals more or less like ourselves. From time to time the stolon has produced special disciplines which have grown into great, flourishing complexes. . . . The stolonic relationship of natural history, or ecology, to the other biological disciplines is of great theoretical and practical significance. Nearly all the important biological problems, especially of a physiological or morphological character, have arisen in the course of simple investigation in natural history and many of the more difficult of them have been turned over to the special disciplines for solution. On the other hand, the ecologist is continually drawing on the methods and resources of physiology, morphology, taxonomy, distribution, etc., in solving his own particular problems of adaptation and behavior.

It is evident that Wheeler's use of the word "ecology," in this connection, is considerably broader than that given it by the societies and journals which bear that name.

Wheeler's metaphor of the stolon seems to me admirable, though it is defective in one respect. For the individual plants or animals which are budded off from a stolon are capable of detaching themselves from the parent stock and becoming independent organisms. Our specialized branches of biology, on the contrary, can not live independently of the parent stock and in so far as they attempt to do so, they languish. (All this Wheeler himself would, of course, have insisted upon.)

We may state this last idea differently by stressing the importance of maintaining the natural history point of view, whatever specialty one may happen to be pursuing. Regarded from this angle, we might consider anyone to be a naturalist who consistently maintained the natural history point of view. This is the point of view which looks beyond the immediate object of one's pursuit and does not lose sight of its relations to a larger whole. It stresses synthesis as a necessary complement to analysis, integration as a necessary complement to differentiation.

The naturalist, as thus conceived, never forgets that he is dealing with organisms dwelling in environments, even though he may be concerned for the moment with cells, chromosomes, genes, sols, gels, ions, unsaturated valencies or what not. He recognizes the autonomy of biology as a science, and does not lose interest in those activities

of organisms which he can not subject to physical or chemical analysis. In general, I think that he will subscribe to the dictum of Dr. Ritter that "the organism in its totality is as essential to an explanation of its elements as its elements are to an explanation of the organism."

I am tempted to add that in the field of taxonomy the naturalist, as thus described, is more likely to be a "lumper" than a "splitter," though I confess that this is merely a wild guess, based upon my notions of the fitness of things. For the "lumper" is a person who recognizes the importance of stressing resemblances as well as differences, of synthesis as well as analysis.

Do I seem to be wandering too far from the subject-matter of this symposium? I think that I am hewing to the line. What can be of more importance socially than the integration of our knowledge—the assimilation of each new discovery to the past acquisitions of our race? On the contrary we may well query whether extreme specialization may not at times become an anti-social process. When it loses its sense of perspective and adopts an esoteric vocabulary and ideology, does it not actually become an eddy moving in the wrong direction?

Even these references to taxonomy really have a very distinct social slant, as I was long ago moved to point out. For the unchecked splitting of genera results not only in creating confusion in the terminology which we are all forced to use, but it destroys what we may call the "verbal clues to the nearer kinships between species." This situation handicaps a group much wider than that of the professional biologists.

It may be pertinent at this point to recall the question which I put before you at the outset: "Is there any present-day need for a society of naturalists?" I do not have in mind merely a question of name. I have in mind the subjects to be discussed by such an organization, and more yet the manner of their treatment. We have our special societies, which now represent almost every minutest subdivision of the life sciences. It is not my object to deplore

the specialization here implied. This seems to be the price which we must pay for advance in science.

Should there not remain, however, a few organizations which specialize, so to speak, in the more general aspects of biology; which maintain consistently the naturalist's point of view? A society is at least conceivable having as its primary object the presentation of programs calculated to be intelligible and interesting to all members of a diversified audience such as the present one. By this I do not have in mind providing popular programs for the laity. That is quite another problem. I am thinking of ourselves. I have in mind the need among workers in diverse branches of biology, for cultivating and extending such common ground as still remains to us in spite of our increasing specialization. It would not be possible or even desirable, to limit the programs of such a society to discussions in the field of general biology. Reports of individual researches might be welcomed as usual, but with certain very important restrictions. The society should insist that every paper admitted to its program must rise above the merely descriptive level, and that its author must make it clear why we should be interested in what he is telling us.

Or is this a counsel of perfection? Perhaps it is. At least, I have often been told so. And yet I am so convinced that the contrary is true that I have bored some of my colleagues for years with my protestations. Not that these persons do not admit the deplorable condition of so many of our scientific programs, but they adopt a defeatist attitude and argue that the situation is incurable.

One is inevitably met with the challenge: How many of our biologists, particularly our younger ones, are capable of interesting a group as diversified as this? I fear it is true that sufficient attention has never been devoted to training our graduate students to be interesting. Since most of them are merely going to be teachers, perhaps this has not been regarded as important. However, I think it might have a salutary effect if we admitted to our an-

nual programs only those who have made some progress in the art of being interesting. Let the impression get around that it is an honor to present a paper at one of our meetings, and that only the more competent men can make the grade. The practice in the past has too often been to accept with thanks anything that is offered. Is not the alternative plan worth more serious consideration? It might shorten our programs, perhaps, but would that be an unmixed evil?

This matter of being interesting includes, of course, something far more than mere literary or rhetorical skill. It includes the ability to see the broader implications of one's discoveries and to present them intelligibly to persons who are not fellow-travelers in one's own particular compartment. If these broader implications are not discernible, the paper does not belong on the program of a society of naturalists at all. There are more highly specialized organizations before which such communications may be presented.

I must add that these later remarks of mine have a much broader application than merely to our hypothetical society of naturalists. The criteria of interest and intelligibility should be applied even to our more narrowly specialized programs. That these criteria are not sufficiently adhered to has resulted in a situation so often expressed in the declaration: "I don't attend the meetings to listen to papers; I go to visit with my friends." Such an attitude is unduly pessimistic, I think, but we must admit that it has considerable justification.

Regarding the kind of material appropriate for the programs of a society of naturalists, I fear that my remarks thus far have been rather indefinite. Suppose that we get down to cases. It is naturally much easier to pick out examples of things that do not belong on such programs than it is to offer helpful suggestions along constructive lines. This because the pages of our technical journals are filled almost exclusively with material of the former class. Here are a half dozen titles which I jotted

down a few days ago from the contents of recent issues of an equal number of leading American biological journals. They are, I think, quite representative ones. As contributions to the literature these papers are all, perhaps, impeccable. But my hypothetical censor would exclude every one of them from the program of a society of naturalists. It is even possible that an intelligent and sufficiently hard-boiled censor would rule that some of these were unsuited for presentation to any audience comprised of more than six persons. Here are the samples:

An analysis of the chromosomes of the two subspecies *Drosophila virilis virilis* and *Drosophila virilis americana.*

A new race of sharp-shinned hawk from Mexico.

Activity-preventing and egg-sea-water neutralizing substances from spermatozoa of *Echinometra subangularis.*

The functional significance of the capillary bed in the brain of the opossum.

Effect of the introduction of the nitro group into the phenol molecule on toxicity to goldfish.

Experimental study of the function of the corpora allata in the grasshopper *Melanoplus differentialis.*

This is no carefully selected list. It represents a fair sampling of the titles which make up the tables of contents of these various journals. They reflect the prevailing modes in biological research. They all probably represent profitable lines of research.

To pick out an equal number of papers to illustrate the kind which I believe to be suitable for presentation before a society of naturalists is much more difficult. Practically nothing of promise in this direction is to be found in any of the six journals from which the preceding list was taken. One thinks at once of the AMERICAN NATURALIST in this connection. But for years the contents of this journal, with the exception of the symposia which it publishes, have been for the most part highly specialized. Many of the contributions might equally well have appeared in one of the journals of genetics. It is interesting to compare the successive volumes of this important periodical from its inception in 1868 to the present day. We have a pageant of the history of biology in America. It is a long way from Morse and Packard and Hyatt and

Cope to Morgan and Jennings and Child and Parker. Nor can we deny that this trend, on the whole, represents progress.

The sort of material that we are looking for now is best exemplified in the subject-matter of some of the symposia, published in the AMERICAN NATURALIST. (I may add, in the subject-matter of some of the symposia of our present meeting.) Such topics as "Adaptation," "Temperature and Life," "The Species Problem," "The Biology of Sex," "The Cell Theory" and "Contributions of the Higher Animals to an Understanding of Human Biology" surely belong to the realm of natural history in the sense which Wheeler had in mind.

I think none of us, however, would wish to restrict our programs to symposia. Single contributions, invited or volunteered, which meet the requirements of relevancy would probably continue to furnish the backbone of the program.

Since I have said so much about relevancy, it seems a fair request that I should cite the titles of some papers which I should expect our naturalist-censor to admit to his program, though it is obvious that the title alone would not guarantee the acceptability of a paper. With some hesitation I offer another list of six titles which I jotted down after a much more prolonged search than that required for the first list. It would have been a much simpler matter to invent a series of such titles, but it is my wish to restrict myself here to actual ones:

Biological effects of population density in lower organisms.
Genetics of quintuplets.
The toleration of solar heat in desert reptiles.
Homing instinct in salmon.
Facts and theories of bird flight.
Survival value of acridian protective coloration.

It happens that this list is predominantly ecological in its complexion. But this was because the majority of available titles which I encountered were ecological ones. I do not see, however, why discussions based upon the

data of almost any one of the recognized sub-divisions of biology should not be relevant to a naturalists' program if properly handled. But the physiologist should not address himself primarily to the physiologist, nor the geneticist to the geneticist, nor the embryologist to the embryologist. Each should phrase his discussion as little as possible in the peculiar vocabulary of his specialty, and should make a determined endeavor to keep in view the broader significance of the data which he reports.

In fact, I seriously question whether such an organization as we have been discussing should be conducted primarily as a publicity channel through which its members may report their very latest series of experiments or observations. If it is really our object to be mutually informative, would not this object be far better achieved if we presented carefully digested reviews covering the general fields in which our particular research problems lie? Could not the detailed reports of progress usually be better left to our published accounts in the journals? Must we really lose caste by serving for the moment as teachers of one another?

Is all this sort of thing possible, or is it just another "Ham-and-Eggs" proposal? While I am not offering any precise mechanism by which these beneficent results could be achieved, I believe that they could be achieved if we really took the matter seriously. It would, perhaps, require the same degree of ingenuity that we all so cheerfully devote to our experimental problems in the laboratory—also, a considerable amount of hard work.

The essence of the plan, of course, is the selection of material for the programs. I confess that the picture of a hard-boiled censor is not a pretty one. I am afraid that he would not last very long in an American scientific society. But some benign selective agency is necessary for the purpose of soliciting appropriate material and rejecting what is inappropriate. Why should it be any more ruthless for a qualified program committee to reject a paper from its program than for the editors of a journal

to reject an unsuitable manuscript offered them for publication? Why indeed, could not this committee assume some of the friendly advisory functions which our editors perform in relation to the contributions offered them? There is often a third alternative besides outright acceptance or rejection.

I am quite aware that the line between topics which are "relevant" and those which are "irrelevant" to a given program must, at times, be very difficult to draw. Particularly is it difficult to judge by the title of a paper. I have in mind one rather recent case in which a man offered a contribution in the field of ichthyology, which turned out, when delivered, to be little more than a fervid eulogy of the government of Soviet Russia. Our censor had momentarily relaxed his vigilance. It seems reasonable to require that a completed manuscript, or at least a detailed summary of a paper, should be submitted in advance, as indeed is often done now.

Finally, it must be admitted that less depends upon the topic chosen than upon the way it is treated, in other words, upon the mental outlook of the speaker. One of the most harassing program numbers that ever drove me from a lecture-room was delivered by a contributor to an important symposium, a man apparently chosen because he was an "outstanding authority" in his particular specialty, but with no regard for his sense of proportion or ability to rise above the level of particulars. Here again, our censor had gone to sleep at the wheel.

On the other hand, a speaker who views his subject *sub specie aeternitatis* can make almost any bit of information illuminating. Such are our great lecturers in biology, men of the caliber of Edmund B. Wilson and G. H. Parker.

I think that you will agree with me that a naturalist who can bring to pass the beneficent things that I have been talking about will be not only a social phenomenon but a most valuable social asset. I do not wish to imply that we have not already made considerable progress in that direction, but I think that we still have a long distance to travel.

THE ETHICS OF ENMITY IN SOCIAL EVOLUTION[1]

PROFESSOR S. J. HOLMES
UNIVERSITY OF CALIFORNIA

IN the chapter of his "Principles of Ethics" on "The Confusion of Ethical Thought" Mr. Herbert Spencer clearly showed that throughout human history mankind has followed two diametrically opposed codes of conduct which he calls the "ethics of amity" and the "ethics of enmity." To many persons the expression "ethics of enmity" may seem to imply a contradiction in terms. We commonly associate amity with goodness, and enmity with evil. The mere suggestion that enmity has a useful function, with an ethics appropriate to it, is apt to arouse at once an inimical reaction. Nevertheless, probably ninety-nine out of every hundred who profess allegiance to an ethics based exclusively upon amity would, if their country were invaded by a hostile army, pay scant attention to the maxim "Resist not evil," and would wholeheartedly and vociferously support measures for inflicting death upon their adversaries. They would do this, moreover, in obedience to the dictates of conscience and in the conviction that failure to support the cause of national defense would be base and highly blameworthy.

Up to, and in some countries within, recent times duelling, as Spencer points out, was supported by the strongest moral sanctions, and a man who failed to challenge one who insulted him was looked upon as a coward and a poltroon. Our code of honor befitting a gentleman has changed. We are no longer under a moral obligation to fight duels, but on occasion collective fighting meets with almost universal approval. Nearly every one would concede without hesitation that the Belgians were morally justified in forcibly resisting the ruthless and unprovoked invasion of their country in 1914. Under the circum-

[1] Read at a symposium on "The Biological Basis of Social Problems" held in honor of Professor William E. Ritter at the meeting of the Western Society of Naturalists, Monterey, Calif., December 20, 1939.

stances, according to the recognized moral standards of mankind, right conduct for the Belgians called for the employment of the ethics of enmity rather than amity toward their foes.

In treating of the ethics of enmity I am concerned not with what conduct is right in the best of all possible worlds, but in the present very imperfect conditions of human life to which we perforce have to adjust ourselves. If we are in the midst of a war that has been unjustly inflicted upon us, it will profit us little to declare that war is an evil and that it is wicked to engage in it. We may concede that war is a great evil and that nations should endeavor by all honorable means to avoid it; but when a country is in the throes of a life and death struggle its citizens must adjust themselves to a real emergency. If I were attacked by a pack of wolves I would feel that it would be quite ethical to kill as many of these animals as possible. From the standpoint of the wolves cooperation in the common cause of attacking my person is highly commendable behavior, the kind of behavior which nature has compelled these animals to follow under penalty of dying of starvation. Since I am under an equal necessity of resisting the wolves, we both espouse the ethics of enmity in our dealings with one another.

When we look out upon the world of living creatures we find numerous instances of different species whose interests are essentially antagonistic. The brown rat and the black rat are keen competitors, and now the one and now the other prevails. Man is attacked by numerous parasites and other maleficent creatures which we deem it quite proper to treat as enemies. We would bestow the highest commendation upon any one who succeeded in exterminating the hookworm, the blood fluke, or the pallid spirochaete. But while we should not feel the slightest qualms about killing off myriads of these inimical organisms, there are numerous people who believe that our conduct would be morally wrong, that "all life is sacred" and that no living creature should be wilfully put to death.

Numerous Brahmans, Jainists and Buddhists of India sincerely endeavor to extend the ethics of amity to all living creatures whatsoever, and many thousands of them die annually from the bites of cobras and other venomous snakes which fail to appreciate the considerate treatment accorded them by their human associates. The costly practices of these Hindu sects are the consequences of simply carrying out the ethics of amity to an extreme though logically consistent degree.

As species of animals go, man can not be said to suffer from any lack of instinctive pugnacity. The trait exhibits itself from the earliest squallings and kickings of infancy to the most advanced age. In the course of his long evolution man's nature has been molded by strife and for strife. Nature has made him a fighting animal. For countless centuries he has carried on an intermittent warfare with members of his own species. His religious beliefs, his ideals and his moral codes give evidence of the prominent place that combat has occupied in his life and thought. His literature is filled with the records of heroic deeds. The "Iliad," the "Odyssey," the "Aeneid," the epics of the Norsemen recount the glorious achievements of conquering heroes, and "Paradise Lost" translates the field of battle to the next world, where it is carried on against the powers of darkness by winged hosts of angels and archangels under the supreme command of the Son of God, with Gabriel and Michael contributing powerful support as members of the general staff. Men like to read about fighting, to see fighting, to play at fighting, as well as actually to engage in combat.

If we ask how man came to be constituted in this fashion, the evolutionist comes forward with a plausible answer. It is an answer very different from those formerly given, which attributed man's bellicosity to the animal side of his nature, the machinations of evil spirits, or the total depravity arising from original sin. The Darwinian evolutionist looks upon man as owing his traits to their survival value in the struggle for existence.

Group pugnacity, as well as the instincts leading to mutual aid, he regards as having been evolved because they contributed to the success of the groups in which they were best developed. Wherever societies have been evolved in the animal kingdom there we find an unusual development of both mutual aid and group pugnacity, as is strikingly illustrated among the ants, termites and the social bees and wasps, in contrast to most non-social insects. These seemingly opposed traits are not really opposed, but complementary. In sub-human ethics the conduct to which they lead is good from the standpoint of the species concerned. Animal ethics is therefore in part an ethics of amity and in part an ethics of enmity. So also is human ethics throughout most of human history, and for essentially the same reasons. If we consider the moral codes of almost any primitive people we shall find that there is one code for consociates and another for aliens. In Deuteronomy, for instance, the Children of Israel are given the following command: "Ye shall not eat of anything that dieth of itself; thou shalt give it unto the stranger that is in thy gates that he may eat it; or thou mayest sell it unto an alien."

Illustrations of the ethics of enmity are everywhere in evidence in the approved codes of nearly all peoples. In the Old Testament they occur in the greatest profusion. During their sanguinary struggles the Children of Israel not infrequently slaughtered not only all the men, but the women and children whom Jehovah delivered into their hands. They gained victories right and left because of the supernatural aid they received in their ruthless wars of exploitation. Theirs was the ethics of a primitive and warlike tribe. Their ethics of amity formulated in the Ten Commandments and the directions for the conduct of life set forth in Leviticus, Numbers and Deuteronomy form a sharp contrast to their ethics of enmity which were exhibited in their treatment of the surrounding peoples whose lands, goods, and women they desired to appropriate.

There is nothing essentially unique in the ethics of the ancient Hebrews. Similar dual codes of conduct are found in hundreds of groups of predatory nomads the world over. As primitive tribes expanded or were consolidated into nations the same dual standards, although often less clearly distinguished, have continued in practice. They are deeply intrenched in the thoughts and customs of all the nations of the earth. Notwithstanding the influence of the great religions of Confucianism, Buddhism and Christianity which have held up ideals of conduct that make no distinctions of nation or race in the duties they enjoin, the ethics of enmity still meets with almost universal approval in practice, even among those who condemn it in theory. The present wide-spread hostility of man to man is the product of powerful forces which our increase of culture and humanitarian spirit has proved powerless to prevent. There can be no doubt that war is now one of the greatest evils of the world. There can also be no doubt, I believe, that strife has played an important part during the evolution of man in molding human nature into conformity with the needs of social life and in making man a moral animal.

As a result of social evolution, and especially the advancement of science, the conditions and effects of war have greatly changed. Instead of promoting the evolution of the human species, war is now a powerful means of undoing the work of civilization. That there is altogether too much enmity in the world is a statement about which there can not be the least doubt. But at the same time it can not be doubted that there are occasions in which we are morally justified in treating other human beings as enemies. If a vessel is attacked by a gang of pirates who, if successful, would probably rape the women and make the rest of the crew walk the plank, the course of right conduct would be to repel the invaders, even if it involved killing the entire outfit. And there are many other situations in which right conduct requires the injury or destruction of other human beings. When an individ-

ual is antagonistic to society, society has a certain justification in being antagonistic to him. Formerly the ethics of enmity was almost exclusively followed in the treatment of offenders. Now efforts are made to reform the criminal and thus to minister to his welfare as an individual. But although reform is a highly commendable aim, the welfare of the individual can not be allowed to take precedence over the interests of society. The welfare of the late Mr. John Dillinger might have been enhanced by allowing him to go scot free to continue his career of killing; but society is justified in checking such a career even at the cost of the well-being of the offender.

In one form or another the ethics of enmity still has a legitimate part to play in the promotion of the general good. This arises from the fact that the relations of human beings, like those of the lower animals, are often antagonistic. We may deplore this fact, but we happen to live in this kind of a world. We gain nothing by closing our eyes to this situation. In fact, we are handicapped in dealing with several moral problems by our failure frankly to recognize the legitimate place that the ethics of enmity still holds in our social life. Most of us give lip service to an unqualified ethics of amity and approve the ethics of enmity on the ground of practical expediency. So long as we preach the one and practice the other will our efforts at moral reform fall short of their full possibilities of good. Our common thinking on the topic before us is hopelessly muddled. This is largely due to the fact that we try to avoid seeing our moral inconsistencies.

The ethics of amity and the ethics of enmity should differ only in their proximate, but not in their ultimate, aim. Both should be concerned with the promotion of human welfare in the highest and best sense of this term. How human welfare may best be promoted is a scientific problem and often by no means an easy one. To solve it aright we need to understand the springs of human action and to be able to explain why human beings go wrong.

In order to cope with human disease we should know how diseases are caused, and why. Likewise, it is only through the knowledge of causes in the sphere of morals that the moral physician will be most successful in affecting cures. At times he will have to employ the ethics of enmity to effect a desired reform as at times a surgeon must apply the ethics of enmity to an offending member by cutting it off. The business of moral reform is one that requires all the scientific knowledge that we possess, and more. It can not be done by simply preaching the duty of brotherly love.

With all our progress we have met with little success in coping with several moral problems. In our dealings with two evils especially, crime and war, we have made almost a complete failure. It is quite clear, I think, that we can not hope for much by simply telling individuals or nations to be good. The reformer must delve deep into the springs of human action and endeavor to understand the causes of anti-social behavior among nations as well as individuals. It is only through a changed human psychology that much can be effected in dealing with either of the evils mentioned, to say nothing of many others. We live in a world in which the ethics of enmity is practiced to a degree out of all proportion to its real need. The resulting evil thus caused is in no way mitigated, and may even be considerably increased, by the fact that the ethics of enmity is followed with entire moral approval and devotion to duty.

Through the action of social forces people are sometimes caught in unfavorable situations from which extrication is very difficult. At present this is true in our economic life, as it is true in relation to war. In both a shortsighted and misguided ethics of enmity is a powerful factor in thwarting our efforts to mitigate these evils. We have altogether too much enmity not only because of the important role which enmity has played in the past, but because of the real need for a certain amount of it at the present time. As the day when the lion and the lamb

will lie down together is not apt to arrive so long as the lion is so constituted that he must either feed upon lamb or die of starvation, so the day when swords will be beaten into plowshares will not arrive as long as there are aggressor nations which pursue their course of domination in utter disregard of justice, liberty and the most solemn promises. No, we are not ready to dispense with the enmities that are still necessitated by the good life. On the contrary, an ethics of enmity adapted to present conditions of civilization and generally agreed to is one of the great needs of the world. In his day the learned Grotius went far toward formulating such a system in his great book on "Rights in War and Peace," but notwithstanding the many attempts to regulate the conditions and to mitigate the barbarities of warfare, the present wanton killing of non-combatants, the disregard of treaties and the rights of neutral nations, the inhuman treatment of conquered peoples, compel us to admit that there has been scarcely a period since the days of early savagery when the ethics of warfare has fallen to so low an ebb.

That the present turmoil is highly disadvantageous to all parties concerned admits of no doubt. The elimination of war has to be a cooperative undertaking which all nations sincerely desire to accomplish. The problem could have been solved long ago had statesmen, with the approval of their nations, seriously and sincerely devoted themselves to the task instead of continually scheming and maneuvering by devious methods to secure some advantage over their rivals. There is little prospect of much improvement in international relations until we have developed the arts of cooperative, instead of competitive, statecraft. For this involves much more than a changed attitude on the part of leaders whose policies are largely a reflection of popular sentiment. The cure for the evils of our misguided ethics of enmity will come but slowly and only as a result of changes wrought in the outlook and attitudes of people in general. To this end the

greatest aid is to be expected from the sciences that will give us a better understanding of the nature of man and the forces that determine his behavior.

I have ventured to comment upon the ethics of enmity because it is the one aspect of ethics which is in greatest need of clarification. We only add to the confusion by trying to cajole ourselves into thinking that it has no legitimate place. We need to put it in order; to understand its course of evolution and the reasons therefor, and to define clearly its scope and present limits of application. Under present conditions of the world it is, I believe, in this field that a scientific ethics will find its greatest opportunity for contributing to the welfare of mankind.

A BIOLOGIST'S APPRECIATION OF RELIGION AS A FACTOR IN SOCIAL EVOLUTION[1]

DR. E. B. COPELAND
UNIVERSITY OF CALIFORNIA

RELIGION is a body of belief accepted by faith, not founded on the experience of the senses. As an element of importance in the history of humanity, it has always included rules of personal conduct. Faith is not in its nature responsible to reason, and religious people have properly denied the right of reason to try to test its articles; more than this, they have often resented such attempts as impious. Freedom of thought and freedom of speech are fundamental American rights. Nevertheless, no longer ago than my memory reaches, freedom of speech on matters of religion was under fairly strict social control, on the reasonable ground that the cherished beliefs of our neighbors were entitled to respect and consideration.

A biologist, as understood in this talk, is one whose scientific work is based on the principle that what can survive survives, at the necessary sacrifice of what can not survive. This is self-evident, to us. But it is the biologist's application of the principle to man that has made it the most distinctive basis of thought during the last eighty years.

The consciousness that man is an animal must have been latent in all humanity. At the same time, man was, and is, the greatest mystery he knows. The sunrise and the thunderbolt have long been explained, sufficiently so that it is the wise, not the ignorant, who still see anything unexplained in them. But man himself remained almost as unexplained as ever, in the general thought of humanity, an insoluble mystery before which the study of law in the universe ceased to be effective. By fixing man's

[1] Read at a symposium on "The Biological Basis of Social Problems" held in honor of Professor William E. Ritter at the meeting of the Western Society of Naturalists, Monterey, Calif., December 20, 1939.

place in zoology, science broke down the greatest barrier to his appreciation of the universal play of cause and effect.

The same general laws responsible for the origin of man have continued to operate on him. Biologists are, of course, concerned with the evolution of later man from his human forebears, but in this study they find themselves on common ground with students of various other kinds. Man's prime initial asset was his intellect, the best in nature, which enabled him to survive and gradually to assume and maintain dominance over the rest of the animate world. During the rise to dominance, selection was focussed on his intellect, because this function was chiefly responsible for his survival. Whenever selection is thus focussed on one function and the correlated structure, they evolve rapidly, as such processes go in nature. I suppose that before the majority of the surviving races of man were differentiated, and before existing man spread over the globe, his intellect reached what we may be pleased to call its present state of perfection. During this early period his conduct, of course, conformed to rules, which favored his survival as an individual rather than as a member of society.

Once man's dominance was secure, his competition for survival was with other men; and in this competition, the intellect of the individual is no longer the most valuable asset. Groups of men could survive in competition with individual men. Thus the social qualifications which enable men to cooperate in stable groups were more important in determining survival than were any minor chance differences in intellect. Herd instinct is a social qualification. The intellect is not. It is individual, in the long run anti-social. If men think together to-day, and are thus united, they are prone to think each for himself to-morrow, and to be disunited, even hostile. On the other hand, just as instincts held together the groups of man's predecessors in whatever measure was good, so man's feelings, partly instinctive and all in part instinc-

tive, have always performed this service for him, even in opposition to the intellect. And his beliefs, more akin to feeling than to knowledge, have always been more effective in this respect than have the intellect or its products, even wisdom.

Let us begin again with most primitive man. He had always an idea of cause and effect. Just as far as his equipment of knowledge let him, he explained phenomena by their causes. So far, the world was natural. But all about him were phenomena he could not so understand. In the absence of understandable, natural causes, he postulated supernatural causes, or agents. These were his gods, many or few, to be placated, eventually, in man's presumption, to be controlled, if only by the manner of his submission. The field recognized as orderly, in which everything was natural cause or effect, grew steadily through the ages, but always permeated and surrounded by the mysterious work of the gods.

Men's common beliefs about their supernatural enemies and eventual friends held men together in groups. Moreover such beliefs involved rules of conduct to placate and appease the gods and particularly to avoid offending them. The resulting common conduct united the believers the more firmly. As the groups with common belief grew larger, and as superstition was restricted and refined and became more worthy of the name of religion, its hold on men gained steadily in strength.

From the beginning, and with ever increasing intensity, men's bodies of belief, their religions, have been in competition for survival. Leaving out of account authority for the belief, the reasonableness of the belief and the truth inherent in the belief—matters which it is not my business to appraise—two elements have determined survival in the competition between beliefs, eventually between religions. These are their effectiveness as social cement, binding and holding men together for common action, and the essential goodness of the associated rules of conduct, their respective moral codes.

If belief were weak or uncertain, it could not hold its adherents during stress; the group must disintegrate even if its members survived; and the belief must disappear. Half-accepted belief has no value at all. But whole-heartedly accepted religion has been the strongest social cement in human experience. Its only rival has been race-loyalty, patriotism, and the two have commonly gone together, the tribe, race or state having its own religion.

Conduct determined survival long before religion began, and still does so. The intellect can appraise a moral code, and find its articles good or bad as their observance is favorable or unfavorable to the prospect of survival. If any religion enjoined practices unfavorable to survival, its believers sooner or later died and the religion disappeared; that has occurred countless times. Naturally, the moral codes of successful religions are much alike, and much like the code successful races would have had to observe in the absence of religion.

While the codes of the biologist, the statesman and a great religion may, and in a measure must be alike, religion has an incalculable advantage in their enforcement. To the individual, religion sanctions its commands with the prospect of eternity in heaven or hell, compared with which a grain of sand hangs in the mouth of the hour-glass while the rewards and punishments of the biologist and of the state run their course. The latter present death as their maximum penalty; but it is as certain for the good as for the bad; religion offers it to the virtuous as the door to an indescribably happier life.

In the brief period of human history, as must have been so in the long period before formal history, religions have continued in competition, and a few have survived and spread because they held men together effectively and their moral codes were fit to survive. Others, even in our experience, have taught bad practices, or practices which with changing conditions became bad; and the evil has been transient, because their badness condemned such

religions to extinction along with their devotees. That is the biological meaning of badness. Good moral codes preserved those who obeyed them and with them the religion of their belief.

This is too simple to need any elaboration before this audience. It is apodictic doctrine, of the type we frankly seek. It is accepted by the historian, the sociologist, the economist, by the body of the people of the Western world. In our own academic circle only one group rejects it, for its simplicity, the philosophers.

The solution of our problem is that, in its supernatural aspect, religion has been the most effective social cement, and thus, at least in considerable parts of history, the most potent factor in social evolution, and that in its moral aspect it has presented and enforced moral codes, very much the same which would have been recognized, but less perfectly observed, without its authority.

Since we interpret the past so confidently, we may be expected to forecast at least the immediate future, and to draw from the past some lessons for to-morrow's use. Here my confidence diminishes. The future begins with the present. There is no question that in our Western cultural world the development of science and the popular assimilation of some of its findings have impaired the hold of religion. And, quoting Spencer: "Few things can happen more disastrous than the decay and death of a regulative system no longer fit, before another and fitter regulative system has grown up to replace it."

Hardly any thinking man will deny that this is the condition to-day. You have only to consider the public attitude toward industry and thrift to realize that the virtues which preserved our grandparents are flouted and scorned. Without the saving virtues, whereby do we hope to survive? Or is humanity going to the dogs?

Well, there are many who hope for "moral rearmament": that we may retrace a little and take up the old way to a better future. Such things have happened. Men foolish enough to be proud of their emancipation from religion have been glad to get back to it under the

scourge of misery. Sixteen hundred years ago, Christianity was welcomed by a very sick, free-thinking world. The Dark Ages followed, but it might have been worse. It might happen again; but we are not yet ready.

Let me quote Spencer again: "Now that moral injunctions are losing the authority given by their supposed sacred origin, the secularization of morals is becoming imperative." The secularization of morals may mean either of two things, or both. One of these is the formulation of an ethic code based on the demonstrable survival value of its articles, and the promulgation of this code by education. Such a code can be apodictic in its essentials, and therefore effective. It puts foolishness in the place of sin in religious codes, and of crime in the law of the state. This sounds weak; but the fact is that, while a man may reject the idea of sin, and take his chance with the law, no man willingly makes himself a fool in his own esteem. The difficulty with this solution of our troubles is not in making the code, nor in proving its soundness, but in teaching it. This solution might or could work; but I am afraid that it will not.

The other method of secularizing morals is by the assumption of complete control by the state. Every state practices this to some extent when it defines a wrong act as a crime. The extension of this practice is contrary to the American idea of personal freedom. The theory of the totalitarian state demands its extension; and some such states control the conduct of the individual in great detail. However repugnant we find this practice, I believe we must grant that a people who break away from the teachings of religion, and permit their morality to become as lax as ours has become, is at a serious, and eventually at a fatal disadvantage in competition with any people at all equal in other respects, which effectively maintains its code of conduct, by whatever means.

Humanity is not going to the dogs. But our particular race is as capable as any other of damning itself by its own foolishness.

OBSERVATIONS ON THE ECOLOGY AND NATURAL HISTORY OF ANURA

I. HABITS, HABITAT AND BREEDING OF *BUFO COGNATUS* SAY[1]

ARTHUR N. BRAGG

(*Continued from page 349, July–August, 1940, issue*)

Ecological Relations of the Tadpoles

The pools in which *Bufo cognatus* breeds are very productive of foods in the limnological sense. The detail of the ecological seasonal succession in them has never been worked out carefully, but, in general terms, it is as follows (see also Barkley and Smith, 1934):

Within a few days after rains fill the buffalo wallows (more or less, depending upon prevailing temperatures), single-celled algae make their appearance and thousands of eggs of small Crustacea hatch. Protozoa and turbellarian worms may be found in large numbers on the jellies of the toads' eggs within twenty-four hours of their production. By the time that the tadpoles hatch or very shortly thereafter, filamentous algae are usually abundant and aquatic insects (principally beetles of the families *Hydrophilidae* and *Dytiscidae* and various bugs) inhabit the pool. Water ferns (Marsilea or Isoetes) are often common. Tadpoles of other species of Amphibia (at least two species of Pseudacris, *Scaphiopus hammondii,* and, if the temperature is not too low, *Gastrophryne olevacea*) may also occur. Flowering plants begin to thrive about the edges of the pool in response to available moisture and these are visited by numerous small insects, some of which often fall into the pool. Feeding upon these insects, small frogs (especially *Pseudacris* spp. and *Acris gryllus*) usually occur, sometimes sparingly but often in abundance. Within a week or two, each pool is a veritable microcosmos, teeming with life ranging in type from bacteria and algae

[1] Contributions from the Zoological Laboratory of the University of Oklahoma, No. 197.

to insects and vertebrates, all in very complex interrelationships with the others. Often, conditions within a pool are kept somewhat in flux by cattle and horses; sometimes a pool which is beautifully clear when the toads breed becomes and remains quite roiled by the stomping of the larger animals. In such cases, the tadpoles seem to get along well, for I have followed hundreds of them through all stages in such pools and have seen them metamorphose.

The toad tadpoles fit into this picture in two different ways: (1) They feed upon algae, remains of insects and any other animal or vegetable matter which becomes sufficiently softened by the action of the water or bacteria. They are, therefore, partially scavengers. In laboratory cultures, they have been seen to feed upon algae, dead flies, flake fish-food, tropical-fish food, cooked rolled oats, dead tadpoles of their own species and, more rarely, calf's liver. (2) They serve as food for predatory insects and tadpoles, as discussed earlier.

In both capacities, they are of some significance to the succession of life in the pool because of their numbers. A single example is enough to bring this out.

The larger of the two buffalo wallows whose measurements were given above was observed carefully almost daily from early February to late May, 1938. Its level fluctuated from approximately seven to twelve inches, but it was never dry. If we assume it to be circular and to have averaged nine inches in depth, then its area was approximately 386 square feet and its volume, 290 cubic feet. *Bufo cognatus* produced two clutches of eggs in this pool on the same night and no others subsequently. Since the number of eggs in a clutch is approximately 20,000 (Bragg, 1937) and since almost all of these eggs hatched, there was an average of over 100 tadpoles to the cubic foot of water in this pool. Similar calculations on another pool gave an average of 770 tadpoles to the cubic foot.

Under these conditions, the struggle for survival must be great and often tends to become more intense as the pool shrinks from evaporation and the tadpoles become larger.

This tendency is lessened, however, by the depredations of predators. That an ecological balance is finally struck between the factors making for survival and those tending toward destruction of the tadpoles is shown by two facts: (1) that numerous larvae succeeded, both here and in comparable situations elsewhere, in passing metamorphosis and (2) the larvae emerged from another pool of a different type after a larval period of almost exactly the same duration as that of the larvae in this particular pool. This shows that the average of the ecological factors in the two places were closely comparable in so far as the toads were affected. Scaphiopus was not nearly so abundant in the second pool, but predaceous beetle larvae were much more numerous.

It is possible that these facts may be correlated with the observation that the tadpoles always remain small. At hatching, the larvae average about 3.0 mm in length, varying approximately between 1.7 and 3.5 mm. Just before metamorphosis, the average head-body length of twenty-two individuals was 11.2 mm, with an average weight (after preservation in 70 per cent. alcohol) of but 0.2 gm. The body as such actually weighed less than this because of the presence of the tail, which exceeds the head and body in length. It should be noted, however, that if there is such a correlation as that suggested, it applies equally well to most other bufonid tadpoles, at least of American species, since all these also always remain small. Even if the consistently small size of toad tadpoles be solely due to genetic factors, this size may well be an evolutionary adaptation to the crowded conditions resulting from the production of large numbers of eggs in relatively small amounts of water. Only further observation can determine with certainty whether this is the case.

METAMORPHOSIS

The length of larval life of *Bufo cognatus* is close to one and one-half months, although unfavorable conditions may lengthen it somewhat, at least in the laboratory (Bragg,

1937a). The following summary of field observations made in the spring of 1938 illustrate this:

Station 1 (buffalo wallows)

March 29	eggs laid.
April 29	many tadpoles of various sizes.
May 14	no tadpoles; thought to have completed metamorphosis and left the pools.
Total time	46 days.

Station 2 (buffalo wallows)

March 29	eggs laid.
March 31	late gastrulation.
April 18	tadpoles very numerous.
May 13	start of metamorphosis; hind-legs well developed, dorsal spots becoming evident, no forelegs.
May 14	Some with forelegs and long tails on or near the bank.
May 15	Many with but stumps of tails; a few as far as two feet from the pool.
May 16	Beginning to range away from the pool; most now showing the red peppering characteristic of the young toads.
May 18	The largest individuals are now from 50 to 60 feet from the pool. These no longer seek to enter the water for protection.
May 20	All that are near the pool are small; larger individuals have left the region of the pool permanently.
May 26	Older individuals found as much as 100 feet from the pool; some are still just emerging.

Total times:

Laying to start of metamorphosis	45 days.
Time consumed in metamorphosis	2 days.[2]
Time that young toads remained close to pool	2 days.

At various times during the period from late March to mid-May, collections of eggs, embryos or tadpoles were made and reared in the laboratory for comparison with the developing young in the pools. In every case, some of the laboratory animals metamorphosed within a few days of the time that their sisters in the field transformed. However, whereas in the field nearly all which did not fall prey to predators lived and metamorphosed at about the same

[2] For about one week prior to this time, the hind legs grew rapidly. Therefore, I mean to indicate that the actual transformation from aquatic to terrestrial existence takes about two days. The whole process of metamorphosis is carried through in about one week.

time, those in the laboratory varied much in rate of development and many in each culture died and were eaten by those that remained. This occurred whether the water was changed frequently or not and whether tap-water or spring-water was used in preparing the cultures. As might be expected from the findings of Adolph (1931) and of Rugh (1934), tadpoles in uncrowded cultures developed better, on the whole, than those in crowded cultures.

The exact cause of these differences in laboratory-grown tadpoles and those from the same clutches which remained in the pools was not investigated. However, two considerations lead me to suspect a dietary factor. (1) All environmental conditions, in all probability, varied more in the field than in the laboratory. (2) In all cultures, some tadpoles early forged ahead of their fellows; one by one the others died, and when they were eaten by the remainder, some of these in turn forged ahead. Finally, out of several hundred, usually not more than a dozen or so eventually transformed; but those which were successful transformed at the same time as their sisters in the field and gave every evidence of being as healthy and vigorous. This suggests that some substance necessary to normal growth and development was available in limited quantities only and that it finally became concentrated in the bodies of the few that went through metamorphosis. Since the greatest difference in diet was a relative scarcity of animal matter in the laboratory cultures, the source of such a substance, if indeed one exist, is probably to be found in animal-food.

Size-variation at metamorphosis is not marked (see Table 1). The head-body length ranges from about eleven to about thirteen millimeters, and the tail is somewhat longer than this. Seldom does a tadpole reach a total length greater than thirty millimeters before transformation begins.

Metamorphosis is quite rapid (see Fig. 7). During the first day, the hind legs which have been present as visible rudiments for some time (since 20–25 mm total length,

TABLE 1

AVERAGE LENGTHS AND WEIGHTS (MM AND GR, TO THE NEAREST .01) OF VARIOUS STAGES OF YOUNG BUFO COGNATUS*

Stage	No. of indiv.	Length			Weight
		Head-body	Tail	Total	
A	22	11.20 +	14.94	26.24	0.20
B	35	12.39 –	16.25	28.64	0.20
		(a)	(a)	(a)	
C	7	12.33	14.93	27.26	
C	47	13.12	14.00	27.12	
C	12	15.13 –	14.00	29.13	0.18
D	102	11.29	0.32	11.61	0.15 –
E	158	12.03 –	(trace)		0.15 +
		(a)		(a)	
F	18	18.47		18.47	
		17.94		17.94	0.56 –
		(a)		(a)	(a)
G (sta. 2) .	12	56.26		56.26	21.77 –
		49.86		49.86	14.77
		(a)		(a)	(a)
G (sta. 4) .	27	44.91		44.91	12.15 +
		43.14		43.14	9.37
		(a)		(a)	(a)
G (total) ...	39	48.49		48.49	15.19 –
		45.22		45.22	11.03

* Those measured while alive are marked (a); others were measured after preservation in 70 per cent alcohol. The stages given are defined as follows: A, ready for metamorphosis, hind legs just beginning to enlarge but no forelegs present; B, start of metamorphosis, hind legs considerably enlarged; C, Two pairs of legs present, tail still long, seeking to leave the water; D, tail but a stub, out of water but very close to edge; E, end of metamorphosis, dispersing in all directions from the pool; F, about one week after dispersal from the pool; G, end of first summer, about four months after metamorphosis.

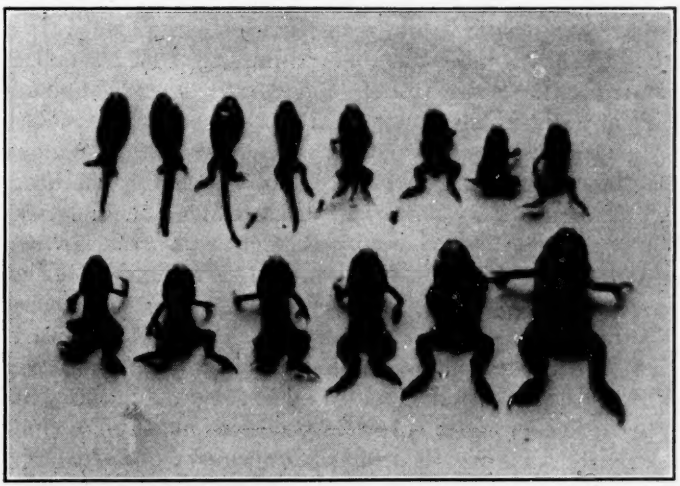

FIG. 7. Stages at and just after metamorphosis of *Bufo cognatus*. The two largest specimens have been out of water approximately one week. Note the evidence of very rapid growth.

Bragg, 1936a) enlarge noticeably, the anterior region of the body and head enlarges and appears to become depressed, and narrow brownish black bars become evident on the dorsal surface of the legs. There is still no noticeable reduction in the length of the tail, which is still used actively in swimming (Table 1, stages B and C). By the end of the first day of active metamorphosis, the animals tend to congregate in large numbers near the bank, become less active unless disturbed, and apparently take little if any food. Within a few hours, the forelimbs break through, sometimes the one on the right preceding that on the left and sometimes, *vice versa,* the hind legs grow rapidly, and there is some decrease in weight (Table 1, stage C).

By the middle of the second day, the color pattern has changed radically. On the dorsal surface, large, dark-colored spots appear. These are usually arranged approximately in pairs, four to eight in number, but with five or six the more common condition. These are the forerunners of the large dorsal spots characteristic of the adults and constitute one of the principal features by which very young toads of this species may be distinguished from toads of other species at the same stage. Often members of certain of these pairs of spots run together in the midline and sometimes one of a pair exceeds its fellow in size. A little later, similar spots, smaller in size, appear along the lateral surfaces, especially in the region of the head. The lateral spots often occur close to the same anterior-posterior level as the dorsal spots, but they vary more than the latter in exact distribution. The forelimbs soon become barred like the hind legs. The ventral iridescence of the tadpoles, described earlier (Bragg, 1936a), has faded by this time, and the under-surface now presents a uniform, just-off-white color. The general tone between the characteristic dorsal and lateral markings is brown or grayish-brown, and this changes abruptly in the ventrolateral regions to the lighter color of the ventral surface. At a magnification of forty, the skin on all surfaces appears pebbly due to tiny wart-like protuberances.

While these changes are occurring, the structure of the head has altered. Larval teeth have disappeared, the mouth has widened, and the eyes have become somewhat more prominent. Also, the behavior of the tiny toads has changed; each now sits with its head out of water at the very edge of the pool and moves very little except when disturbed. The tail is still long and functional, as one easily observes upon approaching a pool ringed with these little toads. At such times, each takes to the water and swims actively away.

Within another few hours, the toads come completely from the water. The tail now begins a very rapid degeneration so that by the end of the second day or early in the third only a small stump remains. Each toad now sits at the very edge, facing the pool into which it will hop if disturbed. Now, however, the hind-legs are functional and the little toad does not go beneath the water; instead, it swims feebly at the surface, usually not getting the dorsal portion of its body wet.

At about this time, a new feature of the coloration develops. This takes the form of brick-red speckles, more or less uniformly distributed over the dorsal and lateral regions. These speckles are quite numerous. On the large dorsal spots, this reddish peppering contrasts sharply with the darker background.

The above description is based upon what is considered to be the average condition. Actually, there is considerable variation among individuals. For example, some of them develop the dorsal speckling before the tail has decreased much in length; in others, it does not appear till the tail is nearly gone. In a few individuals, the mouth may be well transformed, including the development of a prominent tongue, before the tail is appreciably absorbed, though this is not usual. In general it seems that, with the great transformation taking place so rapidly in all portions of the body, the synchrony of the various processes involved in it is not near enough to perfect for all individuals to show exactly the same conditions at any one stage. Transformation in nature is very successful, for

of the several thousands which I have watched passing through the process I know of none which died from physiological causes.

The recently metamorphosed toads start feeding immediately. The food consists of various types of animals which are small enough to swallow. Examination of fecal masses has revealed the following: mites, in considerable numbers; various small beetles, including several small ground-beetles (Carabidae); young snails (Physa); and evidences of several other types of small insects, the remains of which were not recognizable. In the laboratory, toads two days after metamorphosis took gnats, spiders, leaf-hoppers and small beetles. They did not seem interested in any insects as large as or larger than house-flies.

Evidently, feeding sometimes starts before the digestive system is fully prepared, for one fecal mass contained a live mite which had passed through the digestive tract of a toad apparently unharmed.

As might be expected, the size of the body as measured by either weight or length decreases during metamorphosis (Table 1). With the beginning of effective feeding, however, there is a very rapid growth. Within a week after the toads have left the vicinity of the pool after metamorphosis, some individuals have increased over 200 per cent. in weight, although many are much smaller than this. The toads are still tiny, however, the largest weighing less than a gram (after preservation in 70 per cent. alcohol). The animals are much more variable in size now; and this variation continues throughout their first summer if one can judge by the several sizes of young toads collected in the fall.

On October 10, 1938, after a light shower in the morning, young toads were out in numbers in the evening. A total of thirty-nine was collected, twelve within one mile of a known breeding site (station 2) and twenty-seven within a half mile of another (station 4). Since breeding during 1936 and 1937 was not successful, it is certain that these individuals were produced in the spring of 1938; they were, therefore, about four months of age. As measured while

still alive, those from near station 2 varied from 12.0 to 37.2 g. in weight (average, 21.77 g.) and from 48.0 to 63.0 mm in length (average, 56.26 mm). From the other locality the individuals were smaller—weight, 7.7 to 20.3 g. (average, 12.15 g.); length, 36.0 to 56.0 mm (average, 41.91 mm). If we compare the average length of all these (48.49 mm) with the length of adults given earlier, it is at once apparent that these toads were approximately half grown. (Compare, also, Figs. 3 and 8.) If during the second summer the same rate of growth should be maintained, then some individuals, at least, might reach the adult size during the second year. Since there was a great variation in sizes, however, it seems probable that some individuals would not reach maturity for at least another year.

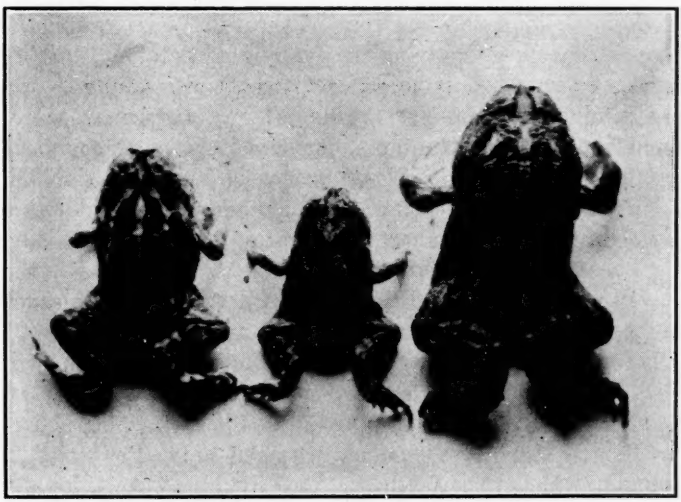

FIG. 8. *Bufo cognatus* approximately four months of age. The specimens shown are the smallest, the largest and one of intermediate size of those taken on October 10, 1938. The largest specimen is more than half the size usually attained at maturity.

Smith (1934) quotes Dickerson as follows: "Judging from the series of decidedly different sizes of this toad (*i.e., B. cognatus*) found in the spring, at least five years must be required for full growth to be attained." My

observations indicate that the different sizes mentioned may not be the result of differences in age alone but also of the availability of food to individuals. In relatively moist summers (like that of 1938) more nights will be spent in hunting for food, and growth will be correspondingly more rapid. During dry summers, however, the young toads remain hidden in burrows, as do the adults, even during the night; and relatively little food is taken. The age at maturity, therefore, varies with individuals and is mostly dependent upon available food.

It is of some interest that of the thirty-nine young *B. cognatus* collected during the evening of October 10, 1938, all but two were females. Of twenty-one young *B. w. woodhousii* collected at the same time, twenty were females. It is also of interest that no adults of *B. cognatus* and only one of *B. w. woodhousii* were seen, although the young of both species were very abundant, much more so, in fact, than the number collected might seem to indicate.

These facts suggest one of two possibilities: (1) the young female toads are more responsive to the presence of a small amount of moisture than are the males; or (2) there were many more females produced during the previous breeding season than males. Both seem equally possible and I have had no opportunity to check which is correct, since this one evening was the only time that *B. cognatus* has appeared during the fall, due to exceptionally dry weather. In any case, it appears likely that the young females are more responsive to the presence of slight moisture than are the adults of either sex.

SUMMARY

Bufo cognatus Say may be found in grassland areas of the Great Plains from southwestern Minnesota southward into Mexico and southwestward to the Imperial Valley, southern California. Its habitat varies in different localities; it is present only in lower, moister areas in arid or semi-arid regions (Texas, New Mexico, Arizona) but in central Oklahoma it occupies the higher portions of the plains. It is largely nocturnal in habit but often appears

during daylight in moist weather, especially during the breeding season. Dry conditions often keep these toads in underground burrows for weeks at a time.

Nothing is known with certainty about the natural enemies of adults. They are probably eaten sparingly by snakes and hawks. Thousands are killed each year by automobiles.

They breed only after rain in spring or summer when the temperature exceeds 12° C. Breeding sites in central Oklahoma include buffalo wallows, flooded fields and the edges of extensive temporary pools. They do not use ditches, "tanks" in pastures, streams nor lakes, and they have never been known to breed in excessively muddy water. Differences in behavior of the sexes during breeding insure that most clutches of eggs will be laid in the location most favorable for development through metamorphosis. The eggs are very numerous (20,000 to each full clutch), and the percentage of hatching is high. Concentration of tadpoles in some pools may exceed 750 per cubic foot of water. Food for the larvae (algae and plant and animal debris) is plentiful in the pools, and large numbers of young often succeed in passing metamorphosis. Their number is limited by the following factors: (1) all pools may dry up and the tadpoles in them die; (2) certain pools may become contaminated and thus kill all eggs and larvae in them; (3) predators often take a heavy toll (predaceous tadpoles of Scaphiopus and larvae of water beetles are known to eat the tadpoles); and (4) at and slightly after metamorphosis, birds (crows and possibly others) sometimes eat the young. The embryos and tadpoles can withstand temperatures in the pools of from near freezing to at least 37° C. and probably more.

Metamorphosis starts about one and one-half months after eggs are laid at a tadpole length of 26 to 29 mm. The young toads have a distinctive color pattern, the major feature of which is four to eight pairs of large dark spots on the dorsal surface and smaller spots on the sides. In two-day-old toads, the whole dorsal surface is dotted with small, brick-red speckles.

Immediately after transformation, the young toads average about 11.0 mm in length, and there is not much variation among them. When at two to three days of age, they disperse from the pool, they are about a millimeter longer. They immediately start feeding and grow very rapidly upon a diet of small insects, young snails and mites. In one week they vary much in size, the larger reaching as much as 20.0 mm in length. In about four months some may be half grown (over 50.0 mm in length), but others may remain much smaller. It is probable that the rate of growth of an individual is primarily dependent upon availability of food. If this be the case, then adult size may be reached in two years by some individuals but not attained by others for three or four years. In any case, difference in size among these young toads is not always indicative of difference in age, as assumed by Dickerson (1913).

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EVOLUTIONARY ALLOMETRY IN THE SKELETON OF THE DOMESTICATED DOG

HYMAN LUMER

WESTERN RESERVE UNIVERSITY AND FENN COLLEGE

INTRODUCTION

IT is well known that within a group of related types of organisms the adult proportions are frequently correlated with total body size. Recent investigations have shown further that in a number of instances the relation between the sizes of corresponding parts in the adults of different types composing such a group conforms to the simple power function

$$y = bx^a$$

where x and y are the sizes of two parts and b and a are constants (Hersh, 1934; Robb, 1935a, 1936; Hamai, 1938).

This expression is identical in form with the law of allometry (Huxley and Teissier, 1936) which has been found in a large number of cases to be a valid empirical representation of ontogenetic growth relations in a single type (see Huxley, 1932). Hence the aforementioned group-phenomenon may be termed "evolutionary allometry."

The investigations cited above deal with size relations in groups of species or higher taxonomic categories. In view of the value of this approach in clarifying taxonomic and evolutionary relationships, it is also of interest to examine its applicability to genetic varieties within a species. For such a study the domesticated dog is exceptionally suitable. Not only does the species comprise a large number of breeds varying greatly in both adult body size and proportions, but it also offers the possibility of supplementing the group investigations with genetic analyses of ontogenetic relative growth in the individual breeds and their hybrids.

Skeletal proportions have commonly been employed as

a basis for the classification of dogs. The descriptive methods of earlier investigators provide adequate diagnostic features for distinguishing the individual types, yet they have proved inadequate as a basis for classifying these into larger subspecific categories, and efforts in this direction have led to considerable disagreement. The problem has recently been clarified to a large extent, however, by the thoroughgoing statistical analysis of Wagner (1930).

The procedure employed by Wagner consisted in plotting various size indices of different breeds against the length of the cranial cavity, which was selected as a measurement representative of body size. For some indices, the points for the various breeds formed a single band, but for the most part two distinct bands were obtained, the breeds occupying each being the same in all cases. From these results Wagner concluded that the species *Canis familiaris* may be subdivided into two major groups, which he designates simply as Groups *a* and *b*.

The present investigation consists primarily of a further analysis of Wagner's data in terms of the law of allometry.

MATERIAL AND METHODS

The data taken from Wagner (1930) on which the present analysis is based include measurements on the skulls of 247 specimens of 28 modern breeds and of 17 European wolves (*Canis lupus*), also measurements on the limb bones of 146 specimens of 18 breeds. The breeds included, in the grouping proposed by Wagner, are as follows:

Group a

1. German shepherd
2. Dachshund
3. Setter
4. Dobermann pinscher
5. Pointer
6. Dingo
7. Poodle
8. Dunker
9. Lapland dog
10. Iceland sheepdog
11. Fox terrier
12. Schnauzer
13. Borzoi

14. English greyhound
15. Large whippet
16. Whippet
17. Rat terrier
18. Bolognese
19. Toy terrier and monkey terrier

Group b

20. Great Dane
21. Saint Bernard
22. Newfoundland dog
23. Bulldog
24. Old-type bulldog
25. French bulldog
26. Boxer
27. Pug
28. Pekingese and Japanese spaniel

It may be noted that in some cases similar breeds have been lumped together; for example, no distinction is made between different breeds of setters or pointers, and such forms as the pekingese and Japanese spaniel are treated as one group. On the other hand, two types are included which do not represent recognized breeds, namely, the large whippet and old-type bulldog. These include a number of specimens markedly larger than the usual whippet or bulldog, and hence separated by Wagner.

In the selection of measurements suitable for analysis, it was found that only those made between accurately determinable landmarks could be successfully used. In this respect most of the cranial measurements given by Wagner (*e.g.*, cranial width, cranial height) are particularly unsatisfactory, since the landmarks involved are only vaguely fixed and, consequently, these measurements are highly variable. For the precise landmarks and techniques employed in making the measurements used in the present investigation, the reader is referred to Wagner's paper.

Although the literature contains a considerable quantity of data collected by other investigators, it was for the most part impossible, because of differences in methods of measurement, to make use of them. Some measurements, however, such as zygomatic width and basilar length of the skull, were found to be fairly uniform in character, and in the analysis of the relationship between these two dimensions, measurements on thirty-one specimens of ancient and prehistoric types, taken

from a number of sources, were included. Also, some of the data of Becker (1923) on the German shepherd were found sufficiently comparable to those of Wagner to warrant their use in determining certain ontogenetic relative growth constants for this breed. The nature of the data used in these two instances will be discussed more fully below.

It can readily be seen that if the law of allometry holds, then a graph of log y against log x should yield a straight line with slope α and y-intercept log b. The constant α is of particular interest since it represents the per cent. increase in y for each 1 per cent. increase in x. For each of the relationships investigated, therefore, the average measurements for each breed were plotted on a double logarithmic grid. Curves were

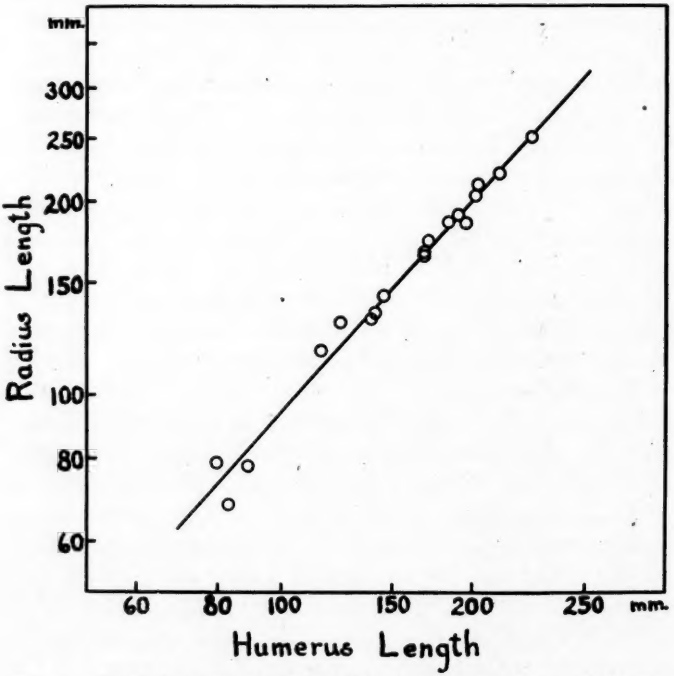

FIG. 1. Double logarithmic plot of radius length against humerus length.

fitted to the data by the regression method of least squares (Feldstein and Hersh, 1935).

Results

The limb bone relations. Three relations involving the limb bones were investigated, namely radius length / humerus length, tibia length / femur length, and length of hindlimb (femur + tibia) / length of forelimb (hum-

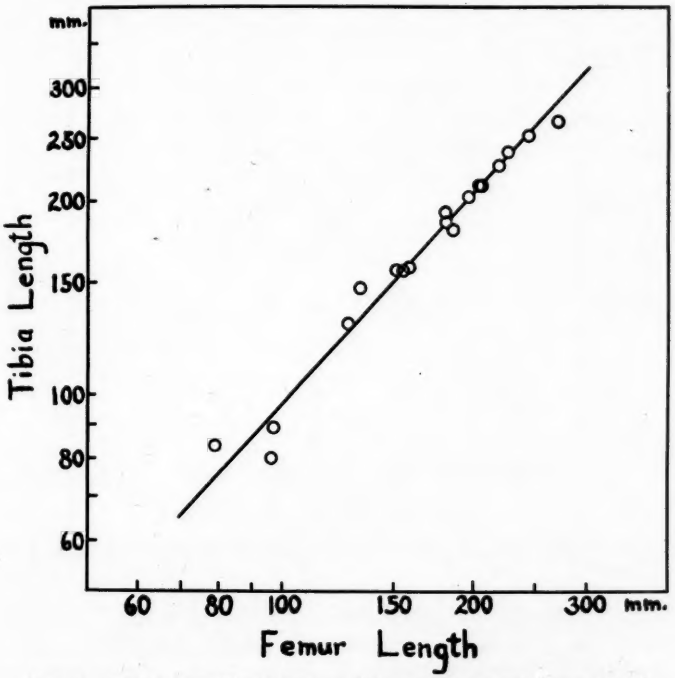

Fig. 2. Double logarithmic plot of tibia length against femur length.

erus + radius). The measurements selected as best representing the lengths of the humerus, radius and tibia are those designated by Wagner as *grösste Länge,* while that used to represent femur length is Wagner's *grösste Trochanterenlänge.* These particular measurements were chosen chiefly because they conform to those

employed by a number of anthropologists in the measurement of primate limb bones.

The curves obtained are shown in Figs. 1–3. It will be noted that in all three cases the points, with few exceptions, fall closely along a single straight line. The

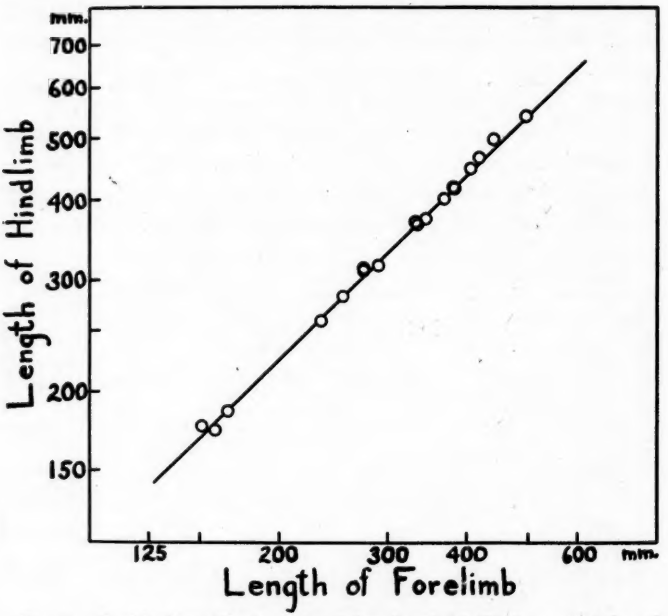

FIG. 3. Double logarithmic plot of length of hindlimb against length of forelimb.

points showing the greatest deviation in Figs. 1 and 2 are those representing the dachshund. In view of the pronounced achondroplasia occurring in the limbs of this breed, these deviations are perhaps not surprising.

The values of a, given in Table I, are somewhat greater than 1 for the first two relations, and slightly less than 1 for the third. These results indicate that among the breeds investigated the lower limb segments tend to become relatively somewhat longer with increasing limb length. On the other hand, there is comparatively little

change in the relative lengths of the limbs, the hindlimb in all breeds being somewhat longer than the forelimb.

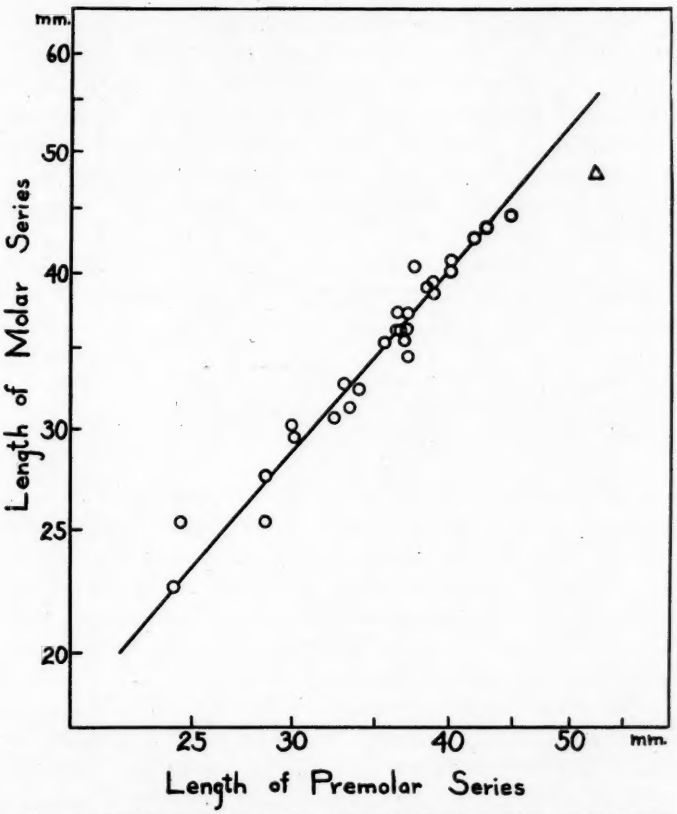

FIG. 4. Double logarithmic plot of length of molar series against length of premolar series in the lower jaw. Triangle represents the European wolf.

The molar / premolar relation. Fig. 4 shows the curve obtained by plotting logarithmically the length of the molar series of the lower jaw against the length of the premolar series. Here again all the breeds concerned occupy a single curve, although the points exhibit an appreciably greater scatter than in the case of the limb relations. The value of α (Table I) is greater than

unity, indicating that with increasing length of the lower jaw, the length of the molar series relative to that of the premolar tends in general to increase.

With respect to this relation, the wolf deviates markedly from the curve characterizing the various breeds of dogs. Not only are the two series of teeth in the wolf greater in absolute length than in any of the dogs, but there is also a difference in proportions, the wolf having a relatively shorter molar series than any type of dog. These differences have also been noted by Wagner (1930).

TABLE I

VALUES OF b AND a FOR THE LIMB BONE, MOLAR/PREMOLAR AND PALATE LENGTH/BASILAR LENGTH RELATIONS

Relation	b	a
Radius length/Humerus length	0.597	1.098
Tibia length/Femur length	0.642	1.090
Hindlimb length/Forelimb length	1.294	0.972
Molar series/Premolar series	0.558	1.161
Palate length/Basilar length	0.506	1.015

The palate length / basilar length relation. In this case, as in the preceding ones, the points for all the breeds form a single curve. As may be seen from Table I, a is approximately equal to 1, and b is about 0.5. That is to say, the palate length is about one half the basilar length in all the breeds. In this respect, the wolf does not deviate from the dogs.

The snout length / cranial length relation. In Fig. 5, the logarithm of the snout length is plotted against the logarithm of the length of the cranial cavity. In this and in the remaining figures, the breeds falling in Wagner's Group a are denoted by open circles and those in Group b by crosses.

It may be noted that the two groups are characterized by distinct curves. The breeds of Group b all occupy one curve, while those of Group a form two separate curves, the upper including breeds 1–16 and the lower breeds 17–19 of the list given above (p. 440). Curves 1 and 2 of the figure approach one another at their upper ends and would intersect, if continued, at about the point representing the wolf.

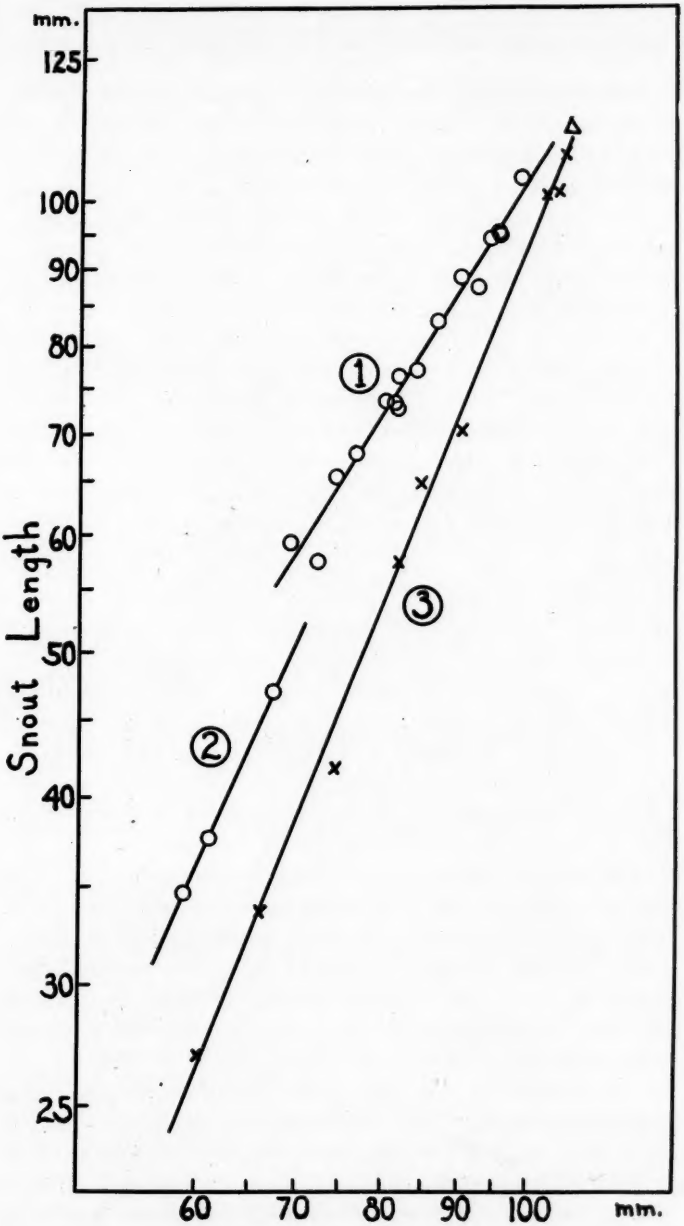

FIG. 5. Double logarithmic plot of snout length against length of cranial cavity. Circles represent breeds in Group *a*, crosses those in Group *b*, and triangle the European wolf.

The values of a, which are given in Table II, are all high, indicating a sharp increase in the relative length of the facial portion of the skull with increasing cranial length. This trend is one which has been previously noted by numerous investigators, and which is known to be parallelled by a similar ontogenetic trend in individual breeds (see for example Becker, 1923; Weidenreich, 1925; Sommer, 1931).

TABLE II

VALUES OF b AND a FOR THE SNOUT LENGTH/CRANIAL LENGTH (SL/CL), SNOUT LENGTH/JAW LENGTH (SL/JL), PALATE WIDTH/PALATE LENGTH (PW/PL), OCCIPITAL WIDTH/BASILAR LENGTH (OW/BL), AND ZYGOMATIC WIDTH/BASILAR LENGTH (ZW/BL) RELATIONS

Relation	I		II		III	
	b	*a*	*b*	*a*	*b*	*a*
SL/CL	0.058	1.624 (1)	0.004	2.249 (2)	0.0009	2.505 (3)
SL/JL	0.347	1.106 (1)	0.204	1.204 (2)	0.0004	2.581 (3)
PW/PL ...	2.764	0.694 (1)	....	.... (1)	5.160	0.596 (3)
OW/BL ...	1.181	0.781 (1)	....	.... (1)	10.893	0.313 (3)
ZW/BL ...	3.345	0.670 (1)	....	.... (1)	8.434	0.504 (3)

Relation	IV		V		VI	
	b	*a*	*b*	*a*	*b*	*a*
SL/CL	.....	.... (3)	....	.... (3)	0.058	1.624 (1)
SL/JL	0.013	1.716 (4)	2.878	0.687 (5)	0.347	1.106 (1)
PW/PL ...	26.011	0.242 (4)	0.393	1.119 (5)	3.659	0.604 (2)
OW/BL ...	4.171	0.560 (4)	0.751	0.877 (5)	2.208	0.640 (2)
ZW/BL ...	20.768	0.351 (4)	0.760	0.961 (5)	5.460	0.553 (2)

Note: The Roman numerals at the heads of the vertical columns refer to the groups listed on p. 455. The numbers in parentheses indicate the number of the curve in the appropriate figure to which the constants apply.

The snout length / lower jaw length relation. The curves obtained for this relation are shown in Fig. 6. The breeds of Group *a* show the same subdivision as in the preceding relation; those of Group *b*, on the other hand, form three distinct curves. Curve 3 includes breeds 27 and 28; curve 4, breeds 23–26; and curve 5, breeds 20–22.

All the curves, with the exception of curve 5, have a slope greater than 1 (see Table II). Curves 3 and 4 have especially high values of a, which means that in these groups the snout length tends to increase considerably in relation to the length of the lower jaw with increasing skull size. In this connection, it may be

pointed out that in the larger breeds of bulldogs the lower jaw is generally less undershot than in the smaller breeds. Thus Wagner (1930) remarks that in the old-

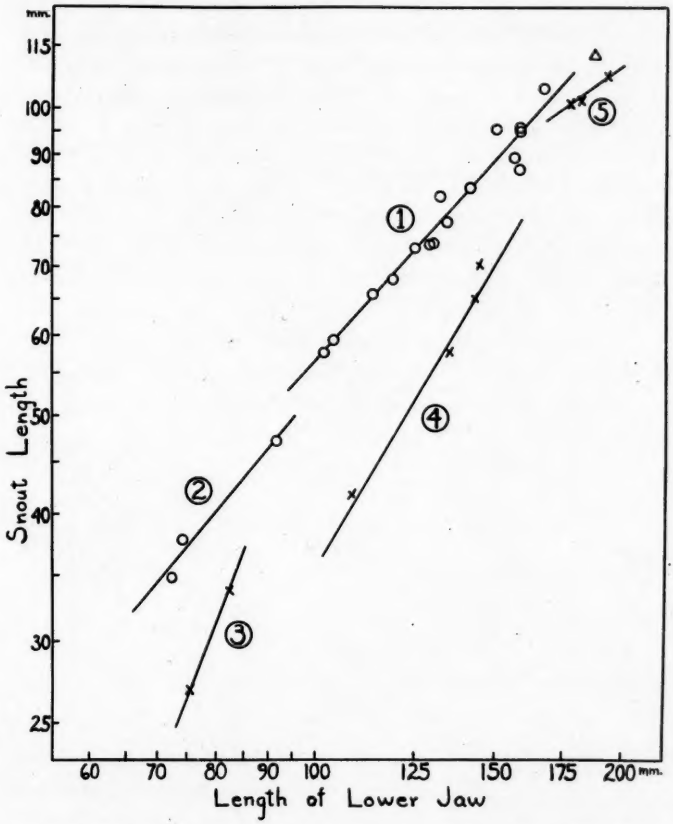

FIG. 6. Double logarithmic plot of snout length against length of lower jaw. Circles represent breeds in Group *a*, crosses those in Group *b*, and triangle the European wolf.

type bulldog, the largest breed of the group, the jaw is either only slightly or not at all undershot.

It should be noted that the point representing the wolf does not in this case fall at the intersection of two curves, but instead appears to conform rather closely to curve 1.

The width / length relations of the skull. Three relationships of this type were investigated, namely palate width / palate length, width of occipital triangle / basilar length, and zygomatic width / basilar length. The resultant curves are shown in Figs. 7, 8 and 9.

It is evident from these figures that the curves obtained are essentially the same in all three cases. Group *b* in each case yields three curves, each of which includes the same breeds as the corresponding curve for the snout length / length of lower jaw relation. Group *a* splits into two curves, of which curve 1 includes breeds 1–12 and 17–19, and curve 2 breeds 13–16. This grouping, it should be noted, does not correspond to the one obtained for Group *a* in the preceding relationships.

In each of the three figures, all the curves except curve 5 have values of α considerably less than 1 (see Table

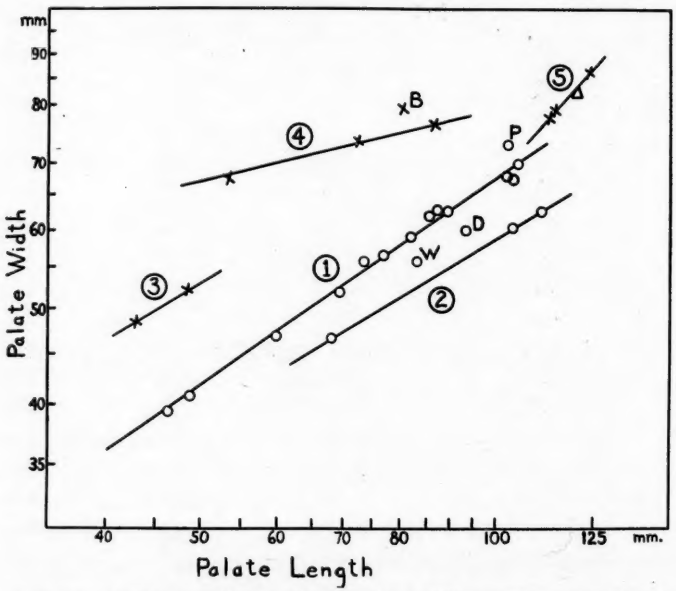

FIG. 7. Double logarithmic plot of palate width against palate length. Circles represent breeds in Group *a*, crosses those in Group *b*, and triangle the European wolf. B—boxer, P—pointer, W—large whippet, D—dingo.

II). There is thus for the most part a very marked decrease in skull width relative to skull length with increasing size, a decrease which is most pronounced in the bulldog group (curve 4). Here again it may be pointed out that a similar change in proportions has been found by numerous investigators to occur in the ontogenetic development of many breeds.

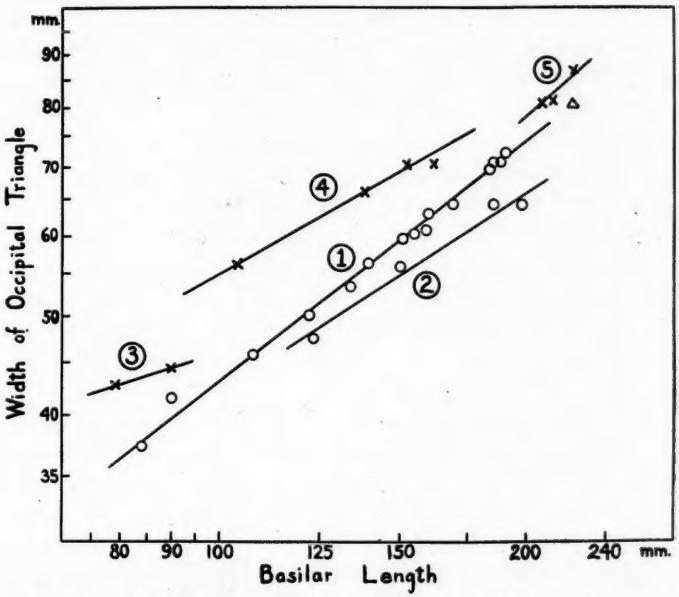

FIG. 8. Double logarithmic plot of width of occipital triangle against basilar length. Circles represent breeds in Group *a*, crosses those in Group *b*, and triangle the European wolf.

In the analysis of the zygomatic width / basilar length relation, measurements on a number of prehistoric and ancient specimens were included. These measurements were taken from the papers of Brinkmann (1924), Hasebe (1924), Hilzheimer (1913, 1932) Noack (1916), Studer (1905), Teodoreanu (1926), and Wagner (1930). In a total of thirty-one specimens, nine distinct varieties are represented. These, together with the number of

specimens of each, are as follows: *C. f. palustris* (10); *C. f. palustris ladogensis* (6); *C. f. matris optimae* (6); *C. f. inostranzewi* (5); *C. f. inostranzewi* (bulldog-like variety) (5); *C. f. intermedius* (3); *C. f. poutiatini* (1); primitive greyhound (1), Inca bulldog (1).

The mean values for each of these varieties are plotted in Fig. 9, where they are denoted by circles marked with crosses. It may be observed that six of the nine points

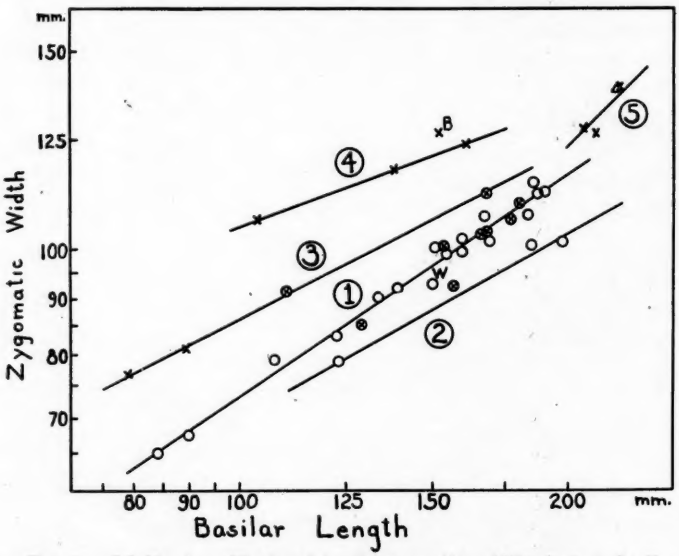

FIG. 9. Double logarithmic plot of zygomatic width against basilar length. Circles represent breeds in Group *a*, crosses those in Group *b*, crossed circles prehistoric and ancient types, and triangle the European wolf. B—boxer, W—large whippet.

conform rather closely to curve 1. Of the remaining three, that representing the primitive greyhound lies close to curve 2, while those representing the Inca bulldog and the bulldog-like variety of *C. f. inostranzewi* fall on curve 3. Hence, so far as is indicated by the available data, the relationships established for the modern breeds appear to hold also for these prehistoric and ancient types.

It is significant that the two bulldog-like forms do not occupy the same curve as the modern bulldog, but fall, together with the pug and the pekingese, on a curve intermediate between curves 1 and 4. Students of the history of the dog are generally agreed that the bulldog is derived from the same stock as the English mastiff, apparently by selection for smaller body size, the Bordeaux dog being regarded by some as an intermediate stage in this process (see Jesse, 1866, Vol. 2, p. 390; also Pötting, 1909). Both these breeds, therefore, should be expected to fall on the same curve as the modern bulldogs. The present results indicate in addition that the prehistoric and ancient bulldog-like forms are most probably not to be regarded as direct ancestors of the modern bulldog, but rather, as Wagner (1930) suggests, as somewhat similar forms which have arisen independently and from an entirely different stock. Similarly, the present results do not support the contention of Pötting (1909) and others that the pug represents a dwarf form of the bulldog.

In connection with these questions, the value of this analysis would clearly be enhanced by the inclusion not only of the mastiff and Bordeaux dog, but also of such dwarf forms as the griffons and Boston terrier. Unfortunately, no suitable data on any of these breeds are available.

There are several distinct deviations from the group curves which merit further consideration. These are, in Fig. 7, the points representing the pointer, large whippet, dingo, and boxer, and in Fig. 9, those representing the large whippet and boxer.

In the pointer, as Marchlewski (1930a) states, a broad facial portion with a marked indentation, or "stop," is regarded by fanciers as an essential feature. A not uncommon defect is "snipeness," in which the snout is narrow and pointed rather than broad and square. The pointer thus represents the result of selection of extreme variants with respect to snout shape, and it is this which

is apparently responsible for its exceptional position with reference to the palate width / palate length relation. Wagner (1930) finds that this breed is exceptional also in the degree of curvature of the face, which he attributes to selection for a pronounced "stop."

The large whippet is a form which occasionally crops up in whippet breeding. Since it is well known that the whippet is historically the product of a cross between the fox terrier and the English greyhound, the occurrence of these large forms is not surprising, nor is the fact that they are intermediate in some respects between the terrier and greyhound groups.

The dingo, or Australian wild dog, has been found by Longman (1928) to differ from other breeds of dogs in its dentition. In particular, the anterior-posterior length of the carnassial in the dingo is greater than 10 per cent. of the condylobasal length of the skull, whereas in all the types of domesticated dogs investigated it is less than 10 per cent. In this respect, according to Longman, the dingo resembles the wolf more closely than it does the domesticated dog. Wagner (1930) finds that the degree of curvature of the face is appreciably less in the dingo than in other dogs with the same skull size. The deviation in proportions of the upper jaw is very probably associated with these differences.

The German boxer, a dog with an extremely broad, short skull, appears to be very closely related to the bulldogs. The available information on this breed, however, does not provide any immediate explanation for its deviations from the bulldog group.

The point representing the wolf falls definitely on curve 5 in Fig. 7 and 9. In Fig. 8, on the other hand, it conforms much better to curve 1.

Allometric tribes. The results presented in the foregoing sections show that the domesticated dog may be subdivided into several groups, each of which is characterized by the fact that for any given relationship all its members fall along a single curve conforming to the

law of allometry. As a designation for any subspecific group distinguished in this manner, the term *allometric tribe* is proposed.

Group *a* comprises chiefly one large subdivision from which, in Figs. 5 and 6, the three smallest breeds, and, in Figs. 7, 8 and 9, the greyhounds and whippets are split off as separate groups. On this basis, Group *a* may be divided into three tribes, of which one is considerably larger than the other two. Group *b* likewise consists of three tribes, making a total of six. These tribes, each designated by the name of a typical form, are as follows:

I Terrier Tribe
German shepherd
Dachshund
Setter
Pointer
Dobermann pinscher
Dingo
Poodle
Dunker
Lapland dog
Iceland sheepdog
Fox terrier
Schnauzer
C. f. palustris
C. f. palustris ladogensis
C. f. matris optimae
C. f. inostranzewi
C. f. intermedius
C. f. poutiatini

II Toy Terrier Tribe
Rat terrier
Bolognese
Toy terrier and monkey terrier

III Pug Tribe
Pug
Pekingese and Japanese spaniel
C. f. inostranzewi
(bulldog-like variety)
Inca bulldog

IV Bulldog Tribe
Bulldog
Old-type bulldog
French bulldog
Boxer

V Great Dane Tribe
Great Dane
Saint Bernard
Newfoundland dog

VI Greyhound Tribe
Borzoi
English greyhound
Whippet
Large whippet
Primitive greyhound

Each of the above tribes is characterized by a set of values of b and α, of which some are distinctive while others are the same as those of other tribes. The extent to which the values of α for a particular tribe differ from unity may serve as a measure of the degree of evolutionary allometry, or the extent to which adult body proportions vary with increasing absolute body size within the tribe. If we use as a criterion the average of the

absolute values of the deviations from unity in all the relations investigated, it is easily shown that the degree of allometry is least in the terrier tribe and greatest in the pug and bulldog tribes.

It should be pointed out that where a tribe is represented by only a few breeds, it is doubtful whether much significance can be attached to the particular values obtained for the constants. This is especially true of the curves characterizing the pug tribe, which for the most part include only two points, and which are therefore to be regarded as merely crude approximations to the true curves, that is, to those which would result if all the breeds of the tribe were included.

Moreover, in the absence of data on a greater number of breeds, certain parts of the present classification must be considered as tentative. For example, it is possible that the distinction between the bulldog and great Dane tribes might prove to be invalid on the inclusion of breeds of intermediate size, such as the English mastiff and Bordeaux dog. At the same time, the results obtained in the analysis of the zygomatic width / basilar length relation indicate that the pug tribe is very probably a valid group, even though it comprises only two of the modern breeds investigated.

Wagner (1930) finds that for a number of relationships the two bands representing his Groups *a* and *b* intersect at approximately the point representing the wolf. He regards this as supporting the theory that the wild ancestral type of dog corresponded to *C. lupus* in size and form. The present results bear out Wagner's finding only in the case of the snout length / cranial length relation. In other respects the wolf generally conforms either to the terrier tribe or to the great Dane tribe. These results, despite the fact that they differ somewhat from Wagner's, appear to support the above theory equally well. More specifically, the wolf may perhaps be regarded as corresponding to the ancestral type of

these two tribes, and the remaining tribes as having been subsequently derived from them.

The relation between b and α. If for any of the relations listed in Table II the values of log b for the different tribes are plotted against the corresponding values of α, the points thus obtained fall approximately along a straight line with negative slope. That is to say, the values of b and α in each case conform approximately to a decreasing exponential function of the form

$$b = Be^{-r\alpha}$$

where B and r are constants. This expression has previously been found to be applicable in similar instances by Hersh (1931, 1934), by Lumer ,1939b), and, in a modified form, by Hamai (1938).

The values of B and r for each curve were determined graphically. Those of r are roughly equal, varying only between 4.61 and 5.37 with an average value of 4.87. On the other hand, B varies considerably, its lowest value being 14.8 and its highest 120. The curves obtained for the different relations are thus a set of approximately parallel lines.

The values of b and α for different relations within a tribe do not yield a distinct curve when plotted as above, but instead fall within a fairly wide linear band.

In a previous investigation (Lumer, 1939a), the author has shown that an inverse relationship between the constants b and α is generally to be expected as a consequence of dimensional connections between them, and that under certain circumstances the relationship would assume the exponential form given above. It was pointed out further that the occurrence of such a functional relationship does not in itself give any clue to the significance of the constants, since the dimensional considerations involved are independent of the particular biological application of the power function in which they appear. Hence it is doubtful what significance is to be attributed to the approximate conformity of the constants in the present case to a decreasing exponential

function. It is, however, of some interest to note that the conformity does exist here as well as in the previous instances.

Ontogenetic relative growth. From the data of Becker (1923), which consist of measurements on the skulls of thirty German shepherds of various ages, the values of the ontogenetic relative growth constants were determined for five different relations. These values are given in Table III, together with the values obtained for the same relations in the terrier tribe, of which the German shepherd is a member.

TABLE III

VALUES OF LOG b AND a, TOGETHER WITH THEIR STANDARD ERRORS, FOR CERTAIN SKULL RELATIONS IN THE TERRIER TRIBE AND FOR THE CORRESPONDING ONTOGENETIC RELATIONS IN THE GERMAN SHEPHERD

	Terrier Tribe		German Shepherd	
Relation	log b	a	log b	a
PW/PL ...	0.442 ± 0.010	0.694 ± 0.005	0.443 ± 0.023	0.687 ± 0.013
SL/JL	-0.459 ± 0.030	1.106 ± 0.014	-0.418 ± 0.020	1.094 ± 0.010
OW/BL ...	0.072 ± 0.011	0.781 ± 0.005	0.179 ± 0.028	0.738 ± 0.013
ZW/BL ...	0.524 ± 0.012	0.670 ± 0.006	0.116 ± 0.059	0.843 ± 0.027
PL/BL	-0.296 ± 0.012	1.015 ± 0.005	-0.114 ± 0.010	0.939 ± 0.004

Comparison of the two sets of values shows that they do not differ significantly for the first two relations. That is, in these instances the ontogenetic curve for the German shepherd effectively coincides with the group curve for the terrier tribe. On the other hand, for the last three relations the differences are well above the borderline of significance.

It should be pointed out that these results are not entirely conclusive, since it is not certain that the measurements of Becker and Wagner are fully comparable. Moreover, in comparisons of this type the situation may perhaps be further complicated by differences in environmental factors, which are known to exert a marked influence on the shape of the skull (see Weidenreich, 1925). The difficulty is increased by the fact that the characteristics of individual breeds change with time as a result of changes in the basis of selection. It is obvious that

in comparing any two groups all these considerations must be taken into account.

Despite these drawbacks, it would nevertheless be of value to determine similarly the relative growth constants for other breeds, and to compare them with one another as well as with the constants for the group curves. However, no comparable data for any other breed are available.

Discussion

The results of the present investigation are essentially in agreement with those of previous studies. Hersh (1934) found that for certain skull relations in the titanotheres all the species investigated form a single curve or band, while for others they form a set of distinct curves, each comprising a single genus. Similarly Robb (1935a) observed that all types of fossil and modern horses fall within a single band with reference to the muzzle length / total skull length relation, while for the relation between length of splints and length of cannon bone (Robb, 1936), two distinct bands are produced, one including the four-toed and three-toed forms and the other the one-toed forms. The results obtained by Hamai (1938) for the relations between height, length, and breadth of the shell in a number of species of snails are in the main similar to those of Hersh.

There arises first the problem of interpreting curves of this type in terms of ontogenetic processes. It is obvious that such group curves will result whenever the ontogenetic relative growth curves of all the members of the group coincide, that is, whenever all have the same values of b and a. The constants of the group curve will of course be the same as those of the ontogenetic curves.

The present results may be most simply explained on the hypothesis that the converse is also true, namely that if for a given relationship the points representing the adults of different types form a single curve, then it

follows that the ontogenetic curves are the same in all the types in question. Some evidence in support of this hypothesis has been presented by Hersh (1934), Robb (1935b), and Lumer (1939b). Hamai (1938), on the other hand, raises certain objections to it, maintaining primarily that the group curves in general represent merely averages of the ontogenetic curves.

To test its validity in the present case would require the determination of the relative growth constants for a number of breeds in each tribe, a procedure for which the available data are very inadequate. The results obtained for the German shepherd seem to militate against the hypothesis, since in three of the five relations investigated the ontogenetic curves deviate significantly from the corresponding group curves. However, as has already been pointed out, these results are not conclusive, and the question should be regarded as still open.

In any event, even if differences in b and α of the ontogenetic curves exist between members of the same tribe, we should not expect them to be nearly as great as those between members of different tribes. Hence it seems justifiable to regard each tribe as a group of breeds relatively homogeneous with reference to genes controlling relative growth, and differing primarily in those affecting adult body size. Or, stated in other terms, the process of evolution within a tribe involves primarily mutations affecting only absolute body size, whereas the evolution of a new tribe involves also mutations producing marked changes in relative growth.

It may be remarked that Wagner (1930) reaches essentially the same conclusion. He distinguishes between size-determining and form-determining genetic factors, and maintains that with respect to the latter, Groups a and b offer different "material" on which the former may operate.

The group curves in the present case differ in one respect from those obtained by Hersh (1934) and Robb (1935a, 1936). The evolution of both the titanotheres

and the horse is characterized by a progressive increase in body size; hence on these curves successive points represent successive stages in time. This is not true of the domesticated dog, for here there has been no such orthogenetic trend. On the contrary, the process of artificial selection through which most of the modern breeds have originated has involved selection for smaller body size as much as for larger. This does not, however, affect the interpretation of the group curves, since the difference lies only in the mode of selection. In both instances the group curves may be regarded as representing the effect of selection for different adult body sizes with no pronounced change in the mechanism of relative growth. Thus the term "evolutionary relative growth" (or its equivalent, "evolutionary allometry") need not, as Hersh (1934) implies, be restricted to those cases in which an orthogenetic trend has occurred. Moreover, the concept may be applied to extant as well as to extinct groups.

From the interpretation presented above, it follows that within a tribe the larger breeds recapitulate in their development (at least approximately) the body proportions of the adult stages of smaller breeds. Such a recapitulation has been found by numerous investigators to occur not only in the dog, but in other domesticated mammals as well (for partial reviews of the extensive literature on this subject, see Becker, 1923; Weidenreich, 1925; Sommer, 1931). These observations have led several investigators to view the condition in dwarf forms as a retention of juvenile characters resulting from developmental arrest.

This concept has been elaborated particularly by Hilzheimer (1926) in his theory of *Verjugendlichung,* according to which arrested development with consequent dwarfing and retention of juvenile proportions in the adult stage occurs not only in dwarf forms, in which it affects the entire body, but also in larger forms, in which only isolated parts are affected. Bolk (1926) has at-

tempted to apply essentially the same idea to man in his fetalization theory, in which he characterizes man as a "sexually mature primate fetus." Bolk's theory has been criticized by Hilzheimer (1927), who maintains that it is valid only for some parts of the human body, and not for the body as a whole.

From the point of view of the present investigation, it is sufficient to point out that where an actual case of retention of juvenile proportions occurs, it is simply a consequence of a decrease in adult body size with no significant change in the course of relative growth. Whether this may properly be called a developmental arrest is debatable, but this point need not be discussed here. On the other hand, where the forms of the same absolute body size exhibit differences in proportions, these must have been achieved through differences in relative growth, or through a cessation of growth in the parts in question before the rest of the body has ceased growing. Unless the latter process is known to have occurred, and this seems at first glance a rather unlikely event, it can not be said in such a case that one form represents a fetal or juvenile stage of another.

The classification of the domesticated dog into allometric tribes proposed here is essentially an extension of that proposed by Wagner (1930). Both of these, however, differ radically from earlier systems, which are based solely on similarities of adult proportions.

The system of classification which has been most widely accepted is that originally elaborated by Studer (1901), which is based on the conception of each of the main prehistoric types as the ancestral form of a group of modern breeds. This classification, in a modified form proposed by Hilzheimer (1933), is briefly as follows:

1. *C. f. palustris* (spitz, terriers, pinschers, etc.)
2. *C. f. intermedius* (hunting dogs)
3. *C. f. matris optimae* (sheepdogs)
4. *C. f. inostranzewi* (mastiffs, bulldogs)
5. *C. f. grajus* (greyhounds).

In the present system of classification, the first three and to some extent the fourth of these groups are combined in the terrier tribe. Similarly Wagner (1930) places all the first three in his Group *a*, on the grounds that the differences between them can be ascribed entirely to differences in absolute body size, which are not an adequate basis for racial distinctions. This contention is fully borne out by the present results. Furthermore, as we have seen above, there is some doubt as to whether the bulldogs may be regarded as having been derived from *C. f. inostranzewi.*

Schäme (1922), on the basis of measurements on individual skull bones, has attempted to classify all dogs into two fundamental types, namely, the *decumanides* type, characterized by short frontals and maxillaries and long parietals and represented by the great Dane, and the *veltrides* type, characterized by long frontals and maxillaries and short parietals and represented by the German shepherd. Götze and Dornheim (1926) sought to verify Schäme's hypothesis statistically by investigating the frequency distributions of certain size indices. They interpreted the resulting frequency curves as being bimodal, and concluded that Schäme's two fundamental types represent ancestral forms, of which most modern breeds are hybrids. The validity of such an interpretation, however, is extremely doubtful, for their curves are very irregular and may in most cases be equally well interpreted as having four or five modes, or, for that matter, as being unimodal. It is evident, therefore, that there is no valid basis for Schäme's system of classification.

A somewhat similar system has been proposed by Marchlewski (1930b), who distinguishes three main types —*C. leineri, C. matris optimae,* and *C. decumanus.* The first includes the greyhounds, the second the sheepdogs and similar forms, and the third the hounds and gundogs. This classification is based on an analysis of skull proportions by the method of least differences, in which

the sum of a number of measurements, each expressed as a percentage of basilar length, is compared in different breeds. Those breeds which differ least in this respect are considered to be most closely related. Since it is conceivable that two skulls differing in many proportions may nevertheless give nearly equal values of the sum used as a criterion, even despite possible correlations between the measurements, the validity of this method is somewhat questionable. Moreover, this approach, like the others discussed above, suffers from the defect of taking into consideration only similarities in adult proportions and neglecting the fact that differences in them may be purely a consequence of differences in absolute body size.

In the present investigation an effort has been made to clarify the relationship between evolutionary changes in body form and the underlying ontogenetic processes. In the determination of body proportions in the vertebrates, an important factor is the activity of the endocrine glands, particularly the thyroid. Thus, as Weidenreich (1925) points out, it has long been known that a high correlation exists between the distribution of goiter and that of brachycephaly in man. Weidenreich also adduces evidence to show that thyroid deficiency is involved in the occurrence of "pugheadedness" (*Mopskopfigkeit*) in domesticated animals. More recently, Dye and Kinder (1934) have demonstrated that thyroidectomy in young dogs, through its effect on ossification of the cartilage bones, results in marked brachycephaly in the adults. The work of Stockard (1931, 1932) also shows a definite association between endocrine function and adult body proportions in dogs. Both Weidenreich and Dye and Kinder suggest that hypothyroidism may be an important factor in the determination of racial types.

The foregoing discussion demonstrates clearly the need for more extensive investigation, particularly of the ontogenetic relative growth in the different breeds, and of the correlation between endocrine function and

relative growth. It would be of especial value to ascertain, by suitable breeding experiments, the relative roles of environmental and genetic factors in producing changes in ontogenetic growth relations, a point on which there has been considerable confusion. It is largely this confusion, it may be noted in passing, which has led Weidenreich and many other investigators, notably Hilzheimer and his students, to adopt a thoroughly Lamarckian point of view in dealing with the problem of the origin of new racial types. Investigations along the lines suggested, together with a more inclusive analysis of adult types, should go far toward providing a solution of the general problem of the relation between ontogenetic development and the evolution of racial types.

Summary

The law of allometry, $y = bx^a$, was applied to measurements on the skulls and limb bones in twenty-eight modern breeds of dogs. The data conform to the equation, yielding in some cases a single curve including all the breeds, and in others two or more distinct curves. On the basis of these results, the various breeds of dogs may tentatively be classified into six *allometric tribes*, each characterized by the fact that for any given relation all its members form a single curve conforming to the law of allometry. This conformity is interpreted as indicating that the breeds within a tribe are genetically relatively homogeneous with respect to ontogenetic relative growth. According to the available evidence, the proposed classification is valid also for ancient and prehistoric types of dogs. The European wolf, however, does not fit into any one tribe. For the same relation in different tribes, the values of b in all cases conform approximately to a decreasing exponential function of a.

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SHORTER ARTICLES AND DISCUSSION

DO HABROBRACON FEMALES STING THEIR EGGS?

In a recent article Spotkov (1938) refers to an early paper by Hase (1922) on sterility in the parasitic wasp *Habrobracon juglandis* (Ashmead). Hase, who at first called his species *H. brevicornis* (Wesmael) but later (1925) corrected this, found that some eggs laid by either mated or unmated females failed to hatch, in one experiment 188 among 317. Spotkov found that when eggs were collected immediately upon being laid and fixed during the first hour of development, almost all (895 among 900) showed normal cleavage. He states that "this is in remarkable contrast to the number of 'sterile' ova obtained by Hase" and suggests that the " 'sterile' ova, as described by Hase, may be produced by accidental puncturing of the eggs by the sting during oviposition." The implication is made, in this comparison of cleavage observations and final hatching percentages, that all or almost all eggs undergoing normal early cleavage will hatch if uninjured by external factors. Spotkov states that the accidental puncture causes loss of protoplasm, but he records no observations as to frequency of puncturing. About 60 per cent. of all eggs would have to be punctured to account for Hase's results.

To the author who has worked with *H. juglandis* for twenty years this idea of the stinging of eggs by mothers came as a surprise. Other investigators were questioned, but none had observed stinging of eggs or thought of it as a possibility.

In 1923 a series of preliminary observations were made on hatchability of eggs from several stocks. Females were transferred to fresh host caterpillars every twenty-four hours, and there was, therefore, ample opportunity for injury to eggs by stinging. Females of all types produced about the same number of eggs per day, so chances for stinging were the same for all. Hatchability was about 80 per cent. for unmated and for outcrossed females, 49.1 per cent. for close-crossed (those mated to related males). Bostian (1935), using females from one stock only, confirmed these results. He found hatchability to be 81 per cent. from unmated females, 83.2 per cent. from outcrossed and 66.8 per cent. from close-crossed. It is difficult to think of any mechanism whereby the type of male to which a female has

been mated would influence the number of eggs which she stings.

In passing, it may be observed that the higher mortality from close-crosses is due to lower viability of those diploid zygotes which are potentially male, produced only in such crosses, and that this phenomenon obtains within the species wherever tests have been made. Inaba (1939) has recently reported it also in *H. pectinophorae* Watanabe.

The author has watched the laying of more than twenty-five hundred eggs of Habrobracon. When they were laid singly each was removed at once and placed on a paralyzed host caterpillar, but when a female laid several in rapid succession they were not disturbed until she had finished. Toward the end of the experiment Spotkov's paper appeared, and during the last part of the work an accurate record was kept on 508 eggs laid by twelve unmated females and every possible case of injury recorded. Twenty-two (4.33 per cent.) were described as having been touched by the sting. F ur of these were undoubtedly injured, since minute oöplasmic extrusions appeared; one hatched and died without feeding, the other three did not hatch. Of the remaining eighteen, eight became adults, one died as a pupa, three as larvae and six failed to hatch. The mothers had been heavily irradiated in this experiment, so that a large percentage of these eggs would not have hatched in any case.

A recent experiment planned for another purpose happens to give a more convincing answer to this question. In order to determine time of death of eggs which, for various reasons, do not hatch, eggs were collected at intervals and placed in the mineral oil "Nujol," where development proceeds normally and conditions can be clearly observed. Numerous observations were made and records kept.

Certain general facts should be mentioned here. An occasional female lays many sterile ova. Data on eggs of such exceptional females are not included in general summaries. There is likewise a tendency on the part of many females to lay "shells," apparently filled only with fluid, which dry up very quickly and become brittle. In one series the percentage of such "shells" was 2.26 for the first ten days of life of the females and 12.06 for the second ten days. Some females produced none, although all were from the same inbred line. If these "shells" result from stinging, it must be concluded that stinging females grow more awkward in their old age and differ innately in degree of awkwardness.

These "shells" are likewise omitted in computing hatchability ratios.

It would be logical to suppose that the percentage of eggs stung would be dependent upon (1) length of time females were left with host, (2) number of eggs on a single host and (3) number of females ovipositing on a given host during a given time. Data are classified from these points of view in Table 1.

TABLE 1

HATCHABILITY PERCENTAGES FOR EGGS OF DIFFERENT GROUPS OF FEMALES. TOTAL NUMBERS OF EGGS ON WHICH PERCENTAGES ARE BASED ARE GIVEN IN PARENTHESES. DATA ARE ARRANGED ACCORDING TO LENGTH OF TIME FEMALES WERE ALLOWED TO REMAIN WITH THE HOST, NUMBERS OF EGGS LAID ON SINGLE CATERPILLARS, AND NUMBERS OF FEMALES OVIPOSITING IN A SINGLE CONTAINER

Females		Eggs on host						Females per container	
		Time			Number			One	Two
No.	Group	1–8 hours	1–24 hours	1–48 hours	1–10	11–20	21–30		
10	33 unmated	94.58 (369)	89.32 (740)	89.43 (246)			88.27 (162)		90.77 (1355)
16	33/11–o mated		90.70 (355)	93.54 (263)					
16	33/11–o unmated				88.30 (265)	88.63 (299)		88.47 (564)	

For eggs collected within eight, twenty-four and forty-eight hours of laying, differences between hatchability percentages of twenty-four- and forty-eight-hour groups from both types of mothers are not statistically significant. The percentage of hatchability for the eight-hour group, however, is significantly higher. This may be due to less chance of being stung or to the fact that the firm yolk-filled freshly laid eggs are less easily injured than embryos when the transfer to the oil is made. Hatchability percentages for eggs grouped according to the number of eggs per host do not differ significantly, nor do those for the containers with one female and with two.

Hatchability percentages obtained by the oil method are higher than those reported earlier in this paper, because this method allows for greater accuracy of observation. In the previous work the difference between eggs and larvae counted directly on the host was taken to represent egg mortality, and minute larvae which died immediately after hatching were often missed. The same sixteen 33/11–o females were used for data from mated and unmated in Table 1. After several days of egg-laying they were

mated and further collections made. Hatchability percentages after mating are those expected from outcrosses, which these matings were.

Each of the 1,226 eggs collected from the 33/11–o females was examined especially for evidence of having been stung. Twelve (0.97 per cent.) were recorded as "possibly injured." They were somewhat wrinkled but contained what appeared to be normal yolk in contrast to the dry "shells" described above. They did not hatch. The mothers in this experiment were young, and only seven "shells" were laid. If it is believed that these two groups represent stung eggs, then 1.54 per cent. (19 among 1,226) were stung.

A final observation of considerable importance in this discussion is that almost every egg which fails to hatch continues development after it has been removed from the container with females and dies at a later embryonic stage. This agrees with Spotkov's observation that almost every egg undergoes cleavage.

From these studies the author concludes either (1) that females sting eggs very rarely or (2) that stung eggs can continue development after such injury and (3) that normal cleavage and even blastoderm formation are no indication of ultimate hatching.

ANNA R. WHITING

UNIVERSITY OF PENNSYLVANIA

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THE REPRODUCTION OF *DUGESIA TIGRINA* (GIRARD)

Dugesia tigrina (synon. *Euplanaria tigrina, Planaria maculata* Leidy) has been known for a long time to reproduce in some habitats exclusively by fission and in others mainly by egg capsules.[1] I have kept animals from both a "sexual locality" and "asexual localities" in laboratory culture for six years and have

[1] W. C. Curtis, *Proc. Boston Soc. Nat. Hist.*, 30: 515, 1902.

attempted to analyze the factors that might control the processes of reproduction. Both lots were exposed to conditions as nearly identical as possible, each lot in several parallel cultures. All the cultures retained their characteristic kinds of reproduction through several generations: the animals from asexual localities continued to undergo fission, while those from the sexual habitat showed regular annual seasons of sexuality and laid cocoons. All attempts to induce the development of genital organs in the asexual animals by changing external factors (amount of food, temperature) were unsuccessful. From these observations I concluded that there must be two distinct physiological races of *D. tigrina,* a sexual and an asexual one.[2]

In a recent paper, L. H. Hyman[3] reports her observations on the occurrence of sexual and asexual animals of *D. tigrina* in natural habitats. She noticed that sexual specimens are found in habitats with considerable movement of water, as in streams or along the shores of lakes and large ponds, where they are exposed to the action of waves. On the other hand, small ponds and other habitats with quiet water contain only asexual worms. Hyman believes that "moving water is the essential environmental factor in the development of sexuality in *D. tigrina.*" She considers the annual recurrence of sexual reproduction in my sexual cultures as no decisive evidence for the existence of a genetically distinct sexual race, "for it might well be that after worms have once attained maturity in nature (under the influence of running water) they might continue to be sexual in laboratory culture, at least to some extent."

Hyman's theory disagrees with the fact that not only animals collected in nature attained sexuality, but likewise those hatched from cocoons in the laboratory and then grown, under usual laboratory conditions, in still water. Hyman finds it difficult to evaluate this result "in the absence of exact data." As detailed records had been omitted from my former paper,[2] I wish to supplement here the data concerning this particular question.

Seven lots of cocoons, deposited in laboratory cultures at various times, were isolated in separate dishes and kept under observation. In all these dishes the animals matured, and in the next breeding seasons laid egg capsules. The cultures gave in every respect the impression of normal sexual cultures, and no decline

[2] R. Kenk, *Biol. Bull.*, 73: 280, 1937.

[3] Libbie H. Hyman, *Trans. Am. Micros. Soc.*, 58: 264, 1939.

in the production of cocoons was observed. Table I gives the time of hatching and that of full maturity for some of these lots.

TABLE I

Animals hatched in the laboratory	became mature and laid cocoons
III/30 to V/29, 1933	I/29 to VI/18, 1934, and again XII/24, 1934, to V/2, 1935
III/24 to VI/4, 1934	VII/23 to IX/3, 1934, and XI/29, 1934, to VI/17, 1935
VI/11 to VII/16, 1934	XII/31, 1934, to VI/21, 1935
VIII/13 to IX/14, 1934	II/7 to VI/21, 1935

Though in the sexual race sexual reproduction occurred in regular annual cycles, fissions were occasionally observed in single individuals during the period of sexual inactivity which coincided with the warmest season of the year. The animals which had fissioned (head and tail pieces) were segregated from the cultures and observed separately. They preserved, however, in every way the characteristics of the sexual race, becoming sexually mature and laying cocoons in the following breeding season.

Fig. 1 represents a typical pedigree of seven cultures, showing the times of sexual reproduction and of fissioning. Four cultures (II, III, IV and VII) were started from cocoons and attained sexuality in the next breeding seasons (in culture III, cocoons were laid also in the late summer, which is rather exceptional). Animals grown from fission products (cultures V and VI) likewise became mature in due time.

From these data it is evident that in the material I worked with (collected in the pond behind the Episcopal Church in Falmouth, Massachusetts) sexuality was not the result of exposure to moving water. It was apparently determined by "internal" factors, *i.e.*, by the genetic constitution of the animals.

I had suggested to Dr. Hyman that the particular ecological distribution of the sexual and asexual animals in nature, the first being found in quiet and the latter in moving water, might indicate an active preference of the two races for their respective habitats. She considers this interpretation impossible, since sexual and asexual animals sometimes are found close together in the same habitat. In this case, however, it remains to be proven by experimental culture that the asexual animals are not simply young individuals of the sexual form or else that the

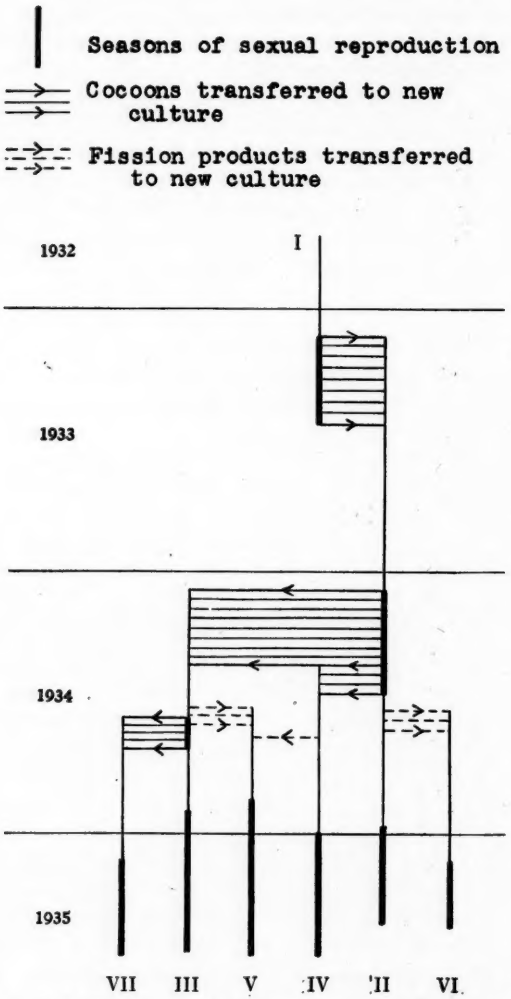

FIG. 1. Pedigree of seven cultures of the sexual race of *Dugesia tigrina*.

separation of the two forms by their habitats is not always possible.

Finally I wish to point out that the conclusions drawn in my paper[2] are, until further investigation, necessarily limited to the

material studied (collected in Virginia and Massachusetts). It is indeed possible that *D. tigrina* in other localities exhibits different physiological characteristics.

Hyman[3] announces that she hopes to test whether asexual "races" of *D. tigrina* can be made sexual by means of running water. It will be interesting to see the results of her experimentation.

ROMAN KENK

DEPARTMENT OF BIOLOGY,
UNIVERSITY OF PUERTO RICO

TRANSLOCATION BETWEEN SPERM AND EGG CHROMOSOMES AS EVIDENCE THAT BREAKAGE PRECEDES UNION

THE problem of the mechanism of induced gene rearrangements has aroused much controversy. At an early stage of attacking this problem two alternatives presented themselves according to Muller (Painter and Muller, 1929). According to one of these, which is more closely analogous to the crossing-over mechanism, the involved chromosomes—non-homologous in the case of translocations—come in contact with or in close proximity to each other in some way, such as lying across one another, and both break at the point of contact or point nearest as a result (direct or indirect) of one common disturbance, *e.g.*, one single ionization. This is essentially the same as the theory advanced by Serebrovsky (1929) and later adopted by Dubinin (1930). The other alternative, which was advocated by Stadler (1932) and later adopted, in part at least, by Muller (1935) (see Dubinin and Khvostova, 1935; Kirssanow, 1937; Muller, 1938, 1939), is that the breaks occur independently as a result of independent causes, *e.g.*, independent favorable ionizations. According to the second scheme, the breakage ends may reunite where they parted—the result being the reconstruction of the original chromosomes—or they may unite in new ways, giving rise to gene rearrangements.

The first of the two alternatives mentioned above is called the "contact hypothesis" and the second the "breakage-first hypothesis." A combination of both of the above alternatives is also conceivable. That is, some gene rearrangements might be produced by one common ionization, while others were produced by independent ones; this might, in fact, even apply to

different breaks involved in the same case of multiple-break rearrangement.

It was the hope of helping toward the settlement of this question that two years ago a large-scale experiment was started, by Muller and the author in collaboration, on the frequency of translocations with two dosages of x-rays, one four times the other. A ring-shaped-X-chromosome as well as a non-ring-X-chromosome were used to facilitate a comparison between the frequencies of double-and multiple-break translocations.

The data obtained show clearly that the total frequency of translocations varies approximately as the 1.5 power of the dosage for the doses used (1000*r* and 4000*r* units). The exponent of the dosage to which the frequency is proportional is definitely higher than one and lower than two. This is to be expected on the breakage hypothesis only. (This work is now being prepared for publication.)

In the experiment mentioned above, for the non-ring-chromosome males from the wild-type, Oregon K stock was used. For the ring-shaped-X-chromosome, Beadle's stock was used in which the males have the so-called Xc^2 ring and the females have attached X's homozygous for yellow. The males from both stocks were x-rayed and mated to virgin females of composition $\bar{y}\bar{y}$ bw e ey, *i.e.*, having attached X-chromosomes homozygous for yellow and their three pairs of autosomes homozygous for brown, ebony and eyeless, respectively; these females also have a Y-chromosome. These matings were carried on in mass cultures in bottles. The F_1 males heterozygous for bw, e and ey and so phenotypically wild-type for Xc^2P_1 males had carried the normal alleles—were backcrossed individually in small vials to virgin $\bar{y}\bar{y}$ bw e ey females. Their progeny were examined for the presence of translocations according to the segregation of characters shown, as explained in the following key:

Translocations involving	Segregation of characters
X–II	all males bw^+; all females bw
X–III	" " e^+; " " e
X–IV	" " ey^+; " " ey
II–III	All flies either bw e or bw^+ e^+; no bw e^+ or bw^+ e
III–IV	" " " e ey or e^+ ey^+ no e ey^+ or e^+ ey
II–IV	" " " bw ey or bw^+ ey^+; no bw ey^+ or bw^+ ey
No translocation	All possible recombinations present of pairs of genes considered two at a time.

Among 11,569 fertile backcross cultures in which Xc^2 males had been used, one gave a progeny showing an unexpected type of segregation of characters. All the males were ebony and the great majority of the females were non-ebony.

A translocation between sperm and egg chromosomes seemed the most likely explanation. This case must have come about in one of the following alternative ways:

(1) An interstitial translocation involving the paternal ring-shaped-X-chromosome and the maternal third chromosome. According to this hypothesis it would be more probable that the ring-shaped X in the irradiated spermatozoon from which the translocation containing F_1 male was derived was broken at two points by the treatment, and that the third chromosome carrying the gene for ebony in the egg which this spermatozoon fertilized happened to have broken spontaneously (not as a result of the x-ray treatment) at one point. Conceivably, however, the ring was broken in one place and the third chromosome in two. After fertilization, the interstitial fragment—deleted from the chromosome having two breaks—became inserted in the gap produced by the breakage of the other chromosome, while the remainder of the chromosome with two breaks joined together again (deletion). The probable direction of exchange above mentioned would be indicated by the presence of a few (2) exceptions among the female progeny (ebony females).

(2) A translocation involving the paternal third chromosome carrying the normal allele for ebony, and the maternal Y-chromosome. The translocation-containing F_1 male will thus have the gene for ebony on his third chromosome and the gene for the normal allele of ebony on his Y-chromosome as a result of the translocation, and so he will be phenotypically non-ebony. But when he was backcrossed to an $\overline{XX}Y$ female of the same stock as his mother, the daughters will get the e^+-containing Y-chromosome, hence being non-ebony, while the sons will get the e-containing third chromosome, being ebony. A few exceptions, arising by non-disjunction between the X and the translocational Y, would not be unexpected here.

Less likely possibilities considered were:

(3) A translocation involving a treated paternal Y and the treated paternal third chromosome. In this case it would have to be assumed that the irradiated spermatozoon carried both X- and Y-chromosomes, due to the occurrence of non-disjunction

either in its immediate formation or in its ancestral cells. Then as a result of the x-rays, a translocation took place involving its Y-chromosome and its third chromosome carrying the normal allele for ebony. The translocation-containing F_1 male will thus have two Y-chromosomes, one of them carrying the normal allele for ebony as a result of the translocation. But that would mean that the ring-X-chromosome would segregate freely with either of the Y-chromosomes, resulting in a larger number of exceptional—non-ebony—as well as numerous ebony females. This result did not obtain, however.

(4) A translocation involving both the Y- and the third-e-containing-chromosomes of the female, which occurred independently of the x-rays. Then in the F_1 male a crossing-over in the nucleus ancestral to the whole of the gonads took place between the paternal ebony-containing third chromosome and the maternal translocational third chromosome, as a result of which the Y-chromosome became connected with the e^+, which was thus transferred to the daughters of the backcross, while the sons got the e-carrying third chromosome. This is obviously an extremely unlikely hypothesis.

Accordingly, the only plausible explanations are the two first mentioned. The decision between them came when males were mated to non-ebony females with attached X's containing y v f car and the males derived from this cross—which, as expected, were non-ebony—were backcrossed to homozygous ebony females (of stock called "rucuca") having separate X's. The offspring showed no sex-linkage of ebony, a fact which proves that their ring-X-chromosome had not been involved in the translocation. This finding rules out the first explanation and thus shows that the correct is the second, namely, a translocation involving the paternal third chromosome and the maternal Y-chromosome.

Spontaneously occurring translocations are so exceedingly rare that the chance of their occurring in any given experiment is practically negligible, and so it is extremely probable that the radiation played some part in the origination of the present translocation. Nevertheless, on the breakage-first hypothesis, the frequency of individual breaks, occurring spontaneously, would be far higher than that of the translocations themselves, since the latter would require at least two breaks at once, a coincidence whose frequency would be only of the order of the square of the individual-break frequency. Thus it is on this

hypothesis, by no means surprising, that there should have been a spontaneous break in one of the maternal chromosomes which underwent recombination with one of the numerous induced breaks that occurred in the paternal chromosomes. That is, the irradiation of the sperm would have greatly facilitated the occurrence of just such a translocation as that which we observed.

On the other hand, on the contact hypothesis, the present translocation would have either had nothing to do with the radiation at all—being one of those exceedingly rare cases that happen spontaneously—or else we should have to invoke for its explanation some kind of considerably delayed after-effect of the irradiation on the paternal chromosomes, other than the effect of breakage, yet an effect of such a nature as somehow to communicate itself from them to the maternal chromosomes. All this seems much more improbable than the breakage explanation, with the premises of which the finding falls naturally into line.

It should further be noted that this case not only serves as an evidence that chromosome breakage precedes union, but also provides further evidence that the union of the broken pieces need not occur during the spermatozoon stage but can be, or must be, delayed until after fertilization. This (in its stronger form) is a conclusion at which Muller, Makhijani and Raychaudhuri (see Muller, 1939) had already arrived on the basis of other results, showing the independence of the frequency of translocations induced by treating spermatozoa from the time factor. Thus, the fact that our results lead to this idea as well must be regarded as increasing the strength of our interpretation as a whole.

In conclusion, we may draw attention to the fact that this case forms the only one yet recorded of a very special type, *i.e.*, a translocation between the paternal and maternal chromosomes. This had for several years been an object expected by those who favor the breakage hypothesis. The author is informed that it was for the obtaining of such a case as evidence for the breakage hypothesis that, while on a visit to the Institute of Genetics, Moscow, Altenburg had proposed the institution of an experiment in which both males and females should be irradiated and bred immediately. Circumstances have till now prevented the carrying out of such an experiment, but the present case has unexpectedly provided some of the desired evidence. It would still be desirable, however, to find the frequency of this phenomenon in control material and in material in which the eggs alone, the sperm alone and both gametes were treated.

SUMMARY

In the course of our work on the relation of translocation frequency to dosage of irradiation and on the relative numbers of double- and multiple- break translocations, one translocation was found between the third chromosome derived from an irradiated spermatozoon and the Y-chromosome derived from the non-irradiated egg which that spermatozoon fertilized. That the Y had not been present in the spermatozoon was shown by breeding tests of the original translocation-bearing individual, since these showed it to contain but one Y-chromosome. Unless we adopt the less probable view that the irradiation had nothing to do with the production of the translocation or that it gave rise to a long-delayed after-effect whereby translocation by contact was brought about, we must conclude that this case arose as a result of union of pieces of a third chromosome broken by the x-rays in the spermatozoon with pieces of a Y-chromosome that happened to have broken spontaneously in the egg. Thus the case argues strongly in favor of the breakage theory of structural change. The hypothesis adopted is not rendered improbable by the rarity of spontaneous structural changes, since on the present view surviving rearrangements require the coincidence of two spontaneous breaks, and this coincidence must be far rarer than the occurrence of only one break.

A. R. SIDKY

SUB-DIRECTOR, ANIMAL BREEDING DEPARTMENT,
MINISTRY OF AGRICULTURE,
CAIRO, EGYPT

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